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是害蟲也是獵物-探究鼠類在避敵反應和農業生態系中的  
雙重角色

Of pests and prey: investigating the dual role of rodents from their  
responses to predation risk to their involvement as pests in agriculture

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## 摘要

鼠類，一個無所不在又分布廣泛的分類群，是許多捕食者的獵物，因此有許多研究試圖研究鼠類被掠食的風險。這些小型哺乳類動物具有躲避掠食者的行為，包括辨別掠食者氣味以避免被取食。然而，不同物種對風險的反應不同，反應機制可能與生理、形態以及生活史特徵有關。在不同的狀況下，物種的行為可能與生活史步調(Pace-of-life)有關，生活史步調從快到慢，以及行為由大膽到謹慎。另一方面，因為齧齒類會造成全球農業巨大損失，也有研究試圖結合被獵食風險來降低鼠害；相較於傳統上利用的化學防治方法，如滅鼠藥的利用，這種方法對環境較為友善，也可降低對非防治目標野生動物的傷害。

本論文的一大部分在檢測掠食者氣味，引發野外族群不同鼠種躲避掠食者行為。另一部分則是調查一個農業地區鼠類對不同作物的影響，以及農民利用滅鼠藥和其他化學防治的比例。

第一個研究計畫中(第二章)，我探討在台灣東部的花蓮，四種鼠類暴露在不熟悉環境，以及非共域掠食者—石虎(*Prionailurus bengalensis*)氣味後的行為反應。這四種老鼠包括三種原生鼠種(田鼯鼠 *Mus caroli*, 赤背條鼠 *Apodemus agrarius*, 小黃腹鼠 *Rattus losea*)，和一種外來入侵種(緬甸小鼠 *Rattus exulans*)。這些老鼠被放置在實驗室內進行連續兩晚的實驗。結果發現鼠類面對掠食者氣味，避敵行為的時間並不會增加。然而，面臨風險，物種間的行為有所差異，體型較小的物種較為大膽，較大的物種則較為謹慎。結果符合生活史步調假說，生活史特徵和抵抗掠食者行為有關。

第二個研究計畫，我使用放棄密度(giving-up density)實驗，配合自動照相機的使用，在有石虎出沒的苗栗縣，研究間接(植被覆蓋程度)與直接(掠食者氣味)被捕食風險訊息如何影響野外鼠類的覓食行為。比較包括原生石虎、引入的家貓(*Felis catus*)和台灣沒出現的短尾貓(*Lynx rufus*)這些掠食者的氣味對於老鼠群聚是否有不同的影響。結果顯示，老鼠造訪食物站和取食的次數，以及種子被取食程度，不會受到任何一種掠食者氣味的影響，但卻會受到微棲地所影響：和空曠暴露的地方相較，有植被覆蓋的棲地，老鼠取食較多種子。另外，自動照相機發現，體型小的鼠種(*A. agrarius*)在行為上較體型大的物種(*R. losea*)大膽。本章結果和第一章結果類似，同樣較支持行為與生活史步調有關。

在第四章中，我訪問苗栗縣農業地區的農民，鼠類危害的程度，相關農害防治措施，農民對鼠類的態度，以及改變農害防治方法的意願。結果顯示老鼠對於稻米的危害最為嚴重，對蔬菜和水果則較無害。此外，只有三分之一的農民指出他們目前有使用滅鼠藥，但有三

分之二的農民有使用其他種農藥。是否使用滅鼠藥和種植作物種類以及鼠害程度有關。和預期相符，當農民覺得鼠類危害很大時就比較會使用滅鼠藥。儘管使用滅鼠藥的農夫不多，但是大部分受訪者對於老鼠持負面的觀感，且與鼠類的危害程度相關。此外，對鼠類有負面觀感的農夫更傾向於會使用滅鼠藥，因此，過去鼠害的經驗與農人的態度決定了防治的措施。同時，滅鼠藥的使用可能反應了鼠害相當嚴重。另一方面，農民雖然支持減低滅鼠藥和殺蟲劑的使用，但並不願意完全不使用這些化學藥劑。適當的獎勵措施可能使農民採用生態友善農法。

本論文的第二章及第三章發現，掠食者的氣味，即使是原生石虎的氣味，也不會引發老鼠的禦敵行為和抑制覓食活動。種間，甚至是個體間行為的差異，會影響對風險的反應。因此，利用創造「恐懼地景」來作為生態防治策略可能不是最有效的方法，未來還需要更了解如何利用掠食者風險為基礎的鼠類防治策略。同時，不同鼠種之間的行為差異，可能造成不同的鼠害問題。根據本論文第四章對農民的調查，開發整合性生態防治措施是有潛力的，但是，如何發展有效的策略還需要更多的研究。

**關鍵字：**老鼠、石虎、捕食風險、行為、取食、大膽、生活史步調、害蟲、態度、滅鼠藥、管理



## Abstract

Rodents, a ubiquitously distributed and pervasive taxonomic group, are common prey to a suite of predators, and as a result have been the subjects of countless studies manipulating predation risk. These small mammals are equipped with antipredator defenses, which includes the ability to discriminate predator odors through olfaction and subsequently modify their behavior to avoid potentially fatal encounters. How different species respond to risk may also vary between species, and these mechanisms may be linked to physiological, morphological and life history traits. Behaviors of species across different contexts may be associated with pace-of-life (POL) following a fast-slow continuum and boldness-shyness axis. Since rodents also cause devastating losses to agricultural industries on a global scale, innovative methods incorporating perceived predation risk to discourage rodents as pests have been the subject of consideration. This method could be an ecologically friendly alternative to conventional chemical approaches, such as rodenticide application, and reduce risks for non-target wildlife.

A major component of this thesis was to test the efficacy of predator odors at instigating antipredator behavioral responses in different species of rodents from wild populations. Another component of this thesis was to survey an agricultural area to understand the impact rodents have on various crops and what proportion of farmers use rodenticides and other chemical-based pest management.

For my first project (Chapter 2), I investigated the behavioral responses of four rodent species in Hualien County, of eastern Taiwan, exposed to a novel microenvironment and cue from an allopatric predator, the leopard cat (*Prionailurus bengalensis*). Three of the wild-caught rodent species were native (*Mus caroli*, *Apodemus agrarius*, *Rattus losea*) and

one invasive (*R. exulans*) and all were subjected to two consecutive nights of experimental trials in a laboratory setting. Rodents did not respond to the predator odor by increasing the amount of time exhibiting defensive behaviors. Instead, inter-specific behavioral variation was observed exemplified by the smaller species performing more behaviors for boldness and the larger species exercising more caution in response to the risky contexts. These results are in accordance with a growing consensus that behavior is linked to pace-of-life (POL); differences in life history traits are associated with behavioral traits following a fast-slow continuum.

For my second study (Chapter 3), I conducted a giving-up density (GUD) experiment complemented with camera traps in Miaoli County, where leopard cats are found, to investigate how indirect (e.g. vegetation cover) and direct (e.g. predator odors) risk cues influence the foraging behavior of wild populations of rodents. I tested whether the odors of the native leopard cat, introduced domestic cat (*Felis catus*), and exotic bobcat (*Lynx rufus*) would have differential effects on rodent communities. Visitation, foraging and seed consumption at the experimental food patches were not affected by any of the predator odors, but instead by microhabitat type; rodents consumed more seeds in food stations under vegetation cover compared to exposed stations. Additionally, based on the camera trap data, the smaller species (*A. agrarius*) demonstrated a higher proportion of behaviors conferring boldness compared to the larger rat species (*R. losea*). These results are similar to those from chapter one, and also largely adhere the hypothesis that behavior is linked to POL.

In Chapter 4, I describe my study where I conducted a survey for farmers in an agricultural area of Miaoli County to investigate the extent of pest-related damage caused

by rodents, pest control practices employed by farmers, their attitudes toward rodents, and willingness to change their pest management. Rodents were reported to be the worst pest for the crop category rice, but not vegetables nor fruit. Furthermore, only about one-third of farmers indicated they currently use rodenticides, whereas around two-thirds apply other types of pesticides. The most important predictors for rodenticide use were type of crop grown and extent of problems caused by rodents. Intuitively, farmers were more likely to use rodenticides if they perceived rodents to be very problematic and cause damage. Despite the low frequency of reported rodenticide use, most participants had negative attitudes toward rodents, with extent of rodent problem having the strongest influence on attitudes. Moreover, participants with negative attitudes toward rodents were found to be more likely to use rodenticides. Therefore, experiential factors, including perceived damage caused by rodents and farmers' attitudes toward the pest likely facilitate their pest control practices. Moreover, the use of rodenticides may be a reactive measure, indicated by the severity of problems and damage inflicted by rodents. Participants expressed support to reduce their usage of rodenticides and pesticides, but were not willing to stop using the chemical products altogether. With adequate incentives farmers may be agreeable to adopting ecologically-based pest management strategies.

In both studies described in Chapter 2 and 3, predator odors did not elicit defensive behaviors and suppress foraging activity, even in response to the native leopard cat cues. Behavioral variation at the species level, and even between individuals, is an important factor that can influence overall responses to risk. Therefore, the application of these direct risk cues simulating the 'landscape of fear' as an ecologically-based management strategy for rodents as pests may not be the most effective and will require further attention to better

understand the capabilities of predation risk-related pest control. Concomitantly, inter-specific behavioral variation occurs between different rodent species, therefore, their roles as pests may not all be equal. Based on the farmer's responses from the survey discussed in Chapter 4 there is potential for the integration of ecologically-based management practices, however, developing effective strategies will require more attention.

**Key words:** rodents, leopard cat, predation risk, behavior, foraging, boldness, fast-slow continuum, pace-of-life (POL), pest, attitudes, rodenticide, management



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## Chapter 1: General introduction

### A brief introduction to rodents

With increasing pressures from human encroachment and activity, many wildlife are facing population declines on a global scale (Schipper et al., 2008; Ripple et al., 2014). Despite many large mammals suffering losses (Dirzo et al., 2014), their smaller counterparts, namely rodents, can withstand and even benefit from modified landscape and anthropogenic impact (Han et al., 2015; Keinath et al., 2017; Tilman et al., 2017). Rodents span the globe and populate every continent except Antarctica. They are the most diverse order of mammals comprising approximately 40% of the class and amounting to well over 2,000 species (Wilson & Reeder, 2005; Burgin et al., 2018). Rodents are characterized by their hardy and flexible bodies, short limbs, long tails, and incisors that grow continually throughout their lives. They also range in size from the pigmy jerboa (*Salpingotulus michaelis*), which is no larger than a human thumb and weighing on average 3.0 g, to the capybara (*Hydrochaeris hydrochaeris*), which can weigh up to 70 Kg (Wilson et al., 2017). Rodents have become adapted to nearly all habitats and lifestyles, such as terrestrial, arboreal, fossorial, and aquatic (Witmer et al., 2014; Wilson et al., 2017). Therefore, they can be adept at climbing, jumping, digging, swimming, and contorting their bodies to fit through tight spaces (Wilson & Reeder, 2005; Pitt et al., 2011).

The expansive distribution of rodents is in part largely due to introductions, some of which were intentional, whereas many were inadvertent (Long, 2003; Drake & Hunt, 2009; Witmer et al., 2014). During periods of human colonization, rodents would often infest ships and were accidentally transported and introduced to locations around the world

(Drake & Hunt, 2009; Renner et al., 2018). Many of these sea-faring rodents were rats belonging to the *Rattus* genus (Drake & Hunt, 2009), which are part of the most speciose family of rodents, Muridae (Burgin et al., 2018). These commensal rodents who have lived alongside humans for centuries are argued to be the original “invasive species” due to their shared global dispersal with colonizing Europeans (Drake & Hunt, 2009). Consequently, the invasions of species of rodents, such as rats (*Rattus* spp.) and mice (*Mus* spp.), have had devastating impacts on native flora and fauna (Towns et al., 2006; Jones et al., 2008). More specifically, invasions of rats have led to regional extirpations of native bird and mammal taxa alike on insular Pacific islands (Lowe et al., 2000; Jones et al., 2008; McCreless et al., 2016). The successful rodent invasions may be attributed to their life history traits, such as high reproductive output, their generalist diet, and ability to survive for extended periods without food (Witmer et al., 2014; Wilson et al., 2017). Moreover, rodents can have a high tolerance for anthropogenic activity and modified landscape (Lowe et al., 2000; Harper & Bunbury, 2015), especially since they can benefit from exploiting human resources, such as food, water, and shelter (Brooks & Jackson, 1973). The nature of this relationship between humans and rodents has resulted in a stigmatized perception and branded the small mammals as pests.

Rodents are not without value though, with native species providing ecological, scientific, and even economic importance (Witmer & Singleton, 2011). They have been used as food and are common in the pet trade. Rodents are also frequently used as model animals in medical research; rats and mice have been tested in countless studies focusing on physiology, neurology, and behavior (Dielenberg & McGregor, 2001; Apfelbach et al., 2005). Native rodents are also integral to their respective ecosystems; facilitating seed

dispersal, nutrient cycling, seed predation, and pollination (Barnett, 2008; Witmer et al., 2014; Wilson et al., 2017). Finally, rodents are common prey to an array of predators, providing sources of food and energy to higher trophic levels.

## **Rodents as prey and the landscape of fear**

The vast range and variety of rodents is analogous with a diverse assemblage of predators. Wherever rodents are natively distributed, so too will be rodent-eating predators, which can include mammalian, avian, and reptilian taxa. Due to persistent predation pressure, rodents have evolved highly developed chemosensory systems designed to discriminate odors of their biological enemies (Masini et al., 2005; Ferrero et al., 2011). If rodents perceive a risk from a predator they will respond accordingly with antipredator behaviors, which can include increased vigilance, avoidance of areas, hiding, motionlessness, decreased activity, and reduced foraging (Apfelbach et al., 2005; Apfelbach et al., 2015; Bytheway et al., 2013; Farnworth et al., 2019). Antipredator responses are costly and can have consequences for immune function, development and reproduction of prey (Creel & Christianson, 2008; Crespi et al., 2013; LaManna & Martin, 2016). These non-consumptive effects (or *risk effects*) can even influence prey population dynamics and community structure (Creel & Christianson, 2008; Gaynor et al., 2019; Figure 1.1). Furthermore, there is increasing evidence to suggest that non-consumptive effects, can account for over half of the predator effects on prey (Preisser et al., 2005; Creel et al., 2009). A framework has been developed, known as the landscape of fear (LOF), which describes the spatial heterogeneity in perceived risk of prey throughout their habitat, with certain areas of a home range perceived as riskier than others generating an unbalanced trade-off between

risk and reward (Laundré et al., 2001). In theory, the framework of predation risk and the LOF may extend beyond research and have applications for pest management (Krijger et al., 2017; Bedoya-Perez et al., 2019).

## **Rodents as pests and the implications**

Rodents are often perceived negatively and as pests because of their capacity to cause damage to infrastructure and destroy crops (Singleton et al., 2010; Meerburg et al., 2009a). For instance, commensal rodents often beget issues for sanitation, food contamination, property damage and disease risk (Buckle & Smith, 2015; Mendoza et al., 2020). Human health risks can be attributed to rodents harboring ectoparasites and having high reservoir competence for certain zoonoses, such as Lyme disease and hantavirus (LoGiudice et al., 2003; Khalil et al., 2016; Young et al., 2017). Rodents, such as species from the *Rattus* genus, cause devastating losses to annual crop yields on a global scale and constitute a major risk for food security (Singleton, 2003; Buckle & Smith, 2015). It is estimated that rodents are responsible for approximately 77 million tonnes of annual food losses (Singleton, 2003; John, 2014). In Asia, rodents are exceptionally problematic for rice production, and this has resulted in food shortages (Singleton, 2003; Meerburg et al., 2009b). Conventional efforts to control rodents typically involve chemical-based products, predominantly anticoagulant rodenticides (ARs) (Ehler, 2006; Meerburg et al., 2008). ARs are not without their limitations though, for instance, rodents may exhibit bait shyness due to neophobia (Prakash, 1988) or develop conditioned aversion through learning to associate the taste and smell of the bait with the harmful effects (Smith et al., 1994; Inglis et al., 1996). Moreover, rodents are capable of developing resistance to commonly used ARs (Lund, 1984; Quy et

al., 1995; Meerburg et al., 2008; Buckle, 2013). ARs can also be extremely problematic for non-target wildlife due to exposure to the poisons (Elliot et al., 2014). Non-target wildlife can directly consume the poisonous baits or experience secondary exposure through the consumption of poisoned animals, which poses the risk of bioaccumulation (Brakes & Smith, 2005; Gabriel et al., 2012; Lohr & Davis, 2018). Therefore, considerations of alternative methods for rodent control are becoming more prominent. Ecologically-based pest management (EBPM), or more specifically ecologically-based rodent management (EBRM), aims to design and implement pest management strategies that reflect the ecology and biology of the pest (Singleton et al., 1999; Brown et al., 2006). EBRM practices can also encourage farmers to work together at specific times during the year and to use non-chemical products, such as traps and organic lures (Brown et al., 2006; Brown et al., 2010). There is also growing support that EBRM should incorporate predation risk and LOF based on the results of studies testing how predation risk cues influence rodent foraging behavior (Singleton et al., 1999; Bleicher, 2017; Krijger et al., 2017; Bedoya-Perez et al., 2019). However, it should not be ignored that responses to predation risk and, in general, the LOF may vary between individuals, populations, and species.

### **Manipulating predation risk and inconsistencies in prey behavior**

The simulation of perceived predator presence, or predation risk, can be manipulated with the use of auditory, visual and/or olfactory cues (Pusenius & Ostfeld, 2002; Apfelbach et al., 2005). Experimental manipulation of predation risk often involves the use of urine, fecal or body odor samples to simulate olfactory cues of the focal predator (Pusenius & Ostfeld, 2002; Brinkerhoff et al., 2005; Apfelbach et al., 2015; Parsons et al., 2018).

Studies manipulating predation risk with the use of predator odors have been performed in both laboratory conditions and in the field (Apfelbach et al., 2005; Takahashi et al., 2005; Bytheway et al., 2013; Carthey & Banks, 2018; Stryjek et al., 2018). However, the effects of predator odors instigating defensive behaviors in rodent prey remains inconclusive, ranging from significant effects (Takahashi et al., 2005; Verdolin, 2006; Carthey & Banks, 2015; Storsberg et al., 2018) to no effect (Bramley & Waas, 2001; Orrock et al., 2004; Cremona et al., 2015). The variability in rodent responses to predator odors may be explained by domestication, intra- and inter-specific behavioral variation, exploitation of cues to gather information about their environment, physiological state, habituation, and rodent community structure (Garvey et al., 2017; Jones et al., 2016; Parsons et al., 2017; Bedoya-Perez et al., 2019). For example, individuals, populations, or even species may demonstrate different behaviors in response to predator odors (Carthey & Banks, 2018; Best et al., 2020). Therefore, how rodent prey respond to predation risk cues may vary depending on the system (i.e., relationships between predators and prey), and thorough investigation is required to test the concepts of predation risk and LOF.

## **Opportunities in Taiwan**

Many species of rodents are widespread throughout the entire island Taiwan. More specifically, populations of rodent species belonging to the Muridae family can be found in both the western and eastern regions of Taiwan, which are divided by the geographical barrier the Central Mountain Range. Rodent communities in Taiwan can have high species richness and be comprised of both native and invasive species. These species also embody variation in morphological and life history traits (Adler, 1995; Qi, 2008; Wilson et al.,

2017). Contrarily, a rodent-eating carnivore, the leopard cat (*Prionailurus bengalensis*), is limited to a handful of areas in western Taiwan. The indigenous leopard cat has been subjected to threats including commercial hunting, habitat loss and fragmentation, and poisoning, which has resulted in its population decline and restricted distribution (McCullough, 1974; Pei et al., 2014). Historically, leopard cats inhabited eastern Taiwan (McCullough, 1974), but now are absent. Therefore, populations of the same species of rodent, such as *Rattus losea*, can be sympatric and allopatric with leopard cats. In the areas where leopard cats and murid rodents do live sympatrically, rodents comprise a large portion of the cat's diet (Chuang, 2012).

Agriculture is a major economic industry in Taiwan, with the production of crops like fruit, rice, and leafy vegetables at the forefront (COA, 2020). This form of anthropogenic activity and its economic importance (COA, 2020) has helped encroach wildlife habitats, which has been the case for leopard cats (Pei et al., 2014). Presently, there is considerable overlap between the leopard cat's range and farmland in western Taiwan, specifically in Miaoli County (24.56° N, 120.82° E) (Pei et al., 2014; Chen et al., 2016; I.N. Best, unpublished data). Residuals of spent pesticides have been found in soil samples from Miaoli County (Liao et al., 2020). Additionally, secondary poisoning of ARs has been reported for rodent-eating raptor species (Hong et al., 2019). Since rodents are a major prey item for leopard cats, multiple pathways of exposure to these chemical products may exist. Therefore, knowledge and understanding of where rodents are problematic for farmers and the farmers' subsequent pest control behaviors is of critical importance to establish risk factors for leopard cats and other non-target wildlife.

## Motivation and research objectives of thesis

The current distribution of rodents and leopard cats in Taiwan permitted experiments to be conducted in both a leopard cat-absent region and a leopard cat-present region. Moreover, because populations of the same species of rodents inhabit both sides of the island, I could test predictions toward their behavioral responses and assess consistency. In eastern Taiwan, where leopard cats are absent, I was interested in investigating the behavioral responses of multiple species of rodents to a novel microenvironment and leopard cat odors. This experiment could also provide information on whether the populations of these wild rodents are naïve to leopard cat cues. In Miaoli County of western Taiwan, where leopard cats are present, I was able to perform field experiments testing the effect of leopard cat odors, as well as other predator odors for a comparative approach, along with indirect risk cues (e.g. microhabitat variation). This design provided the opportunity to test the relative importance of different risk cues (direct vs. indirect), and whether rodents will respond to odors of their sympatric predators. These findings could also establish a baseline for the efficacy of applying the predation risk framework to rodent management. Since multiple rodent species inhabit both eastern and western regions of Taiwan and were included in both studies (chapter 2 and 3), I could also examine inter-specific behavioral variation and whether the behavioral traits of the rodents are associated with life history traits and pace-of-life (POL).

Finally, due to the extensive agricultural activity in Miaoli County, which overlaps with leopard cat habitat, and lack of knowledge of current farmer pest control behaviors, I sought to evaluate the importance of rodents as pests in agriculture, the extent of both rodenticide and pesticide usage, and support from farmers for modifying their pest control

practices. Based on these findings, I could determine agricultural profiles that may reflect risks for leopard cats, as well as the feasibility of proposing EBRM.

A conceptual roadmap for the studies/ chapters, the concepts included in each chapter, and the associations between chapters is presented in Figure 1.2. The main research questions of this thesis are as follows:

1. Will rodents respond to odors of an allopatric predator? Will rodents that live sympatrically with predators respond to their odors?
2. Will there be intra- and inter-specific behavioral variation between rodents in response to risk? Will this variation be associated with pace-of-life following a fast-slow continuum?
3. What is the role of rodents as pests in the agricultural area of Miaoli County? To what extent are rodenticides and pesticides used and would farmers be willing to change these control methods?
4. Is there potential for applying the predation risk framework for rodent management?

## **Organization of thesis**

This thesis has been divided into five chapters. Following a general introduction described in chapter 1, the original work of three studies is presented in chapters 2 to 4 (Figure 1.2) to answer the questions pertaining to roles of rodents as prey and as pests.

In chapter 2, multiple behavioral responses of four species of wild-caught rodents were examined in laboratory experimental trials in eastern Taiwan. All animals were exposed to a novel microenvironment and odor from the allopatric leopard cat. I tested for both intra-

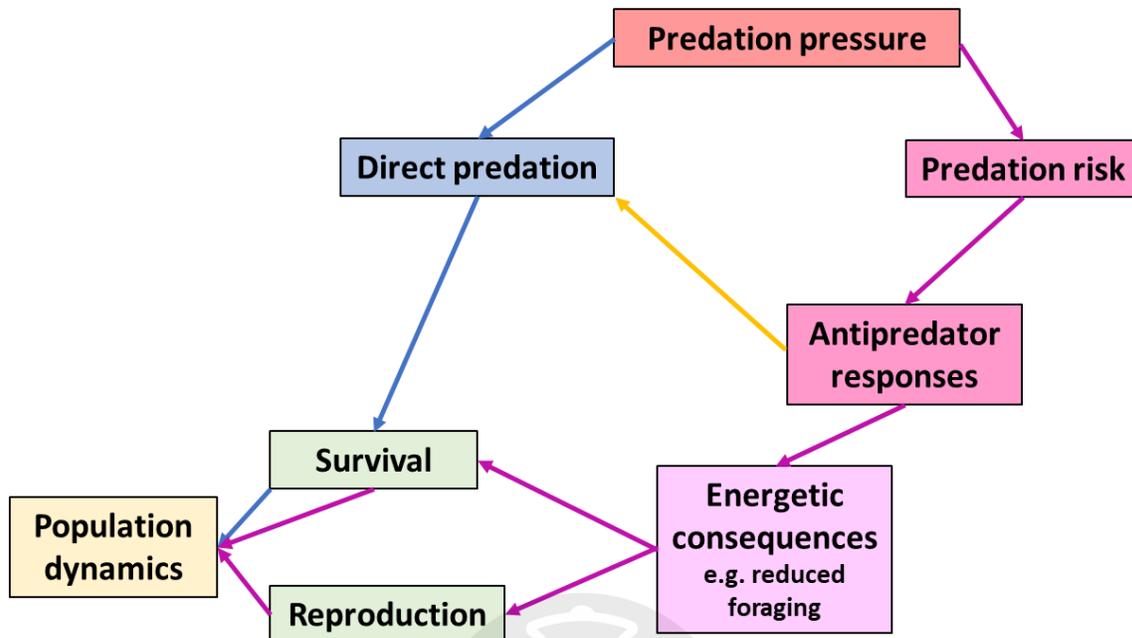
and inter-specific behavioral variation and whether there was a link between behavior and POL, as well as habituation effects.

Chapter 3 focuses on a study that was conducted in the field in Miaoli County of western Taiwan, where leopard cats are currently distributed. Based on the results of chapter 2, I wanted to determine if rodents familiar with leopard cats would display defensive behaviors to the cat's odor. I employed a giving-up density (GUD) experiment complemented with camera traps to investigate how direct (predator odors) and indirect (microhabitat) cues influence rodent foraging and spatial behavior. Similar to chapter 2, I also tested for inter-specific behavioral variation following a fast-slow continuum of POL.

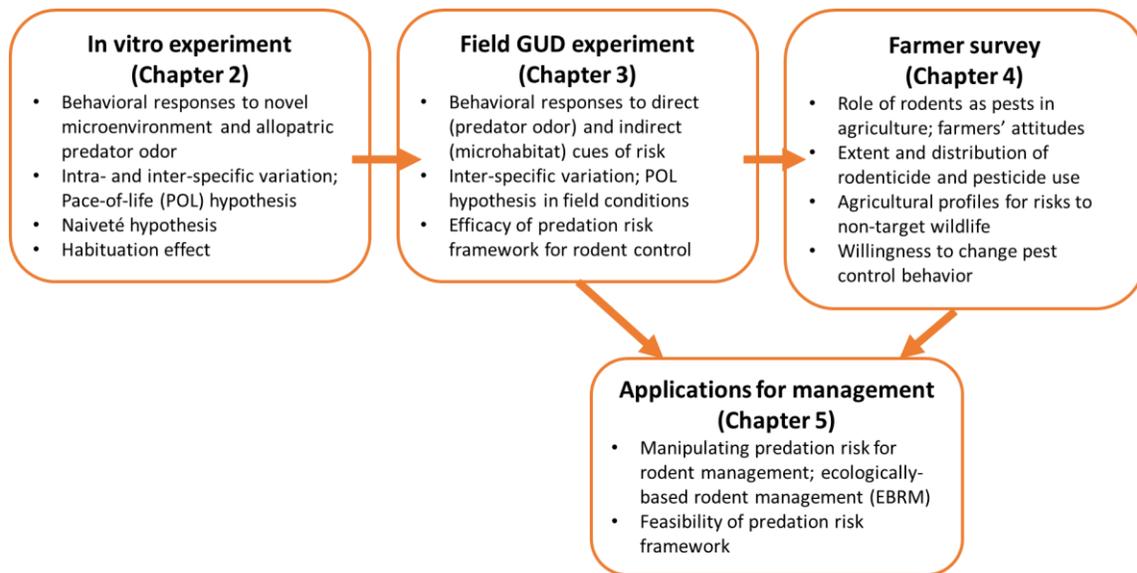
In chapter 4 I describe the survey I conducted for farmers in the agricultural areas of Miaoli County to examine which pests are problematic for farmers, the extent of pest-related damage rodents inflict, attitudes towards rodents, and pest control behaviors. I also assessed willingness of farmers to modify their pest control practices, namely using less or stop using chemical products. An objective of this study was to also generate agricultural profiles that represent risks to non-target wildlife.

Lastly, in chapter 5 I deliberate on the main conclusions from chapters 2 to 4 and consider directions for future work.

## Figures



**Figure 1.1.** Conceptual pathways of predator effects. Predation pressure can result in direct predation, illustrated by blue arrows, and have effects on survival with consequences for population dynamics. Predation pressure can also give rise to predation risk and incite antipredator responses, illustrated by purple arrows, with non-consumptive effects on survival and reproduction and subsequently prey population dynamics. If predation pressure is too high or antipredator responses too weak, direct predation can result, illustrated by the feedback arrow (orange). Arrows extending from ‘Survival’ and ‘Reproduction’ are thinner Energetic consequences via antipredator responses are just one example of non-consumptive effects. Adapted from Creel & Christianson, 2008.



**Figure 1.2.** Conceptual roadmap of thesis. The three main chapters of the thesis are presented (chapters 2-4), with potential application from chapters 3 and 4 discussed in chapter 5. Arrows indicate relationships between experiment/ study, e.g. the linkage between POL and behavior reported in both chapter 2 and 3. Main concepts and hypotheses tested are listed for each component/ chapter.

## **Chapter 2: Bigger doesn't mean bolder: behavioral variation of four wild rodent species to novelty and predation risk following a fast-slow continuum**

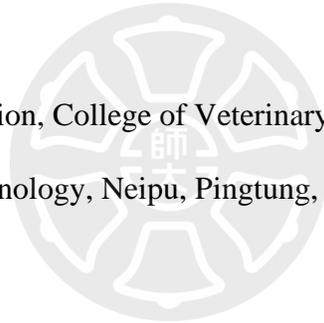
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**Abstract**

Understanding how wild species respond to novel situations with associated risk can provide valuable insights for inter-specific behavioral variation and associations with pace-of-life (POL). Rodents, a globally distributed and diverse taxonomic group, have been the subjects of countless studies emulating risky situations. Controlled laboratory experiments with a focus on wild-caught species provide the opportunity to test fine-scale behavioral responses to contexts of risk with ecological implications. For example, assessing the importance of predator cues eliciting antipredator responses, as well as whether wild rodents embody behavioral plasticity and repertoires, illustrated by habituation and variation in behavioral traits, respectively. In this comparative study, I examined multiple behavioral responses of four rodent species in eastern Taiwan (three native species *Mus caroli*, *Apodemus agrarius*, *Rattus losea*, and one invasive, *Rattus exulans*) exposed to an unfamiliar microenvironment and novel cue from an allopatric predator, the leopard cat (*Prionailurus bengalensis*). All wild-caught animals were subjected to two consecutive nights of experimental trials in a laboratory setting. Behavioral responses to a novel situation during the first trial differed between species; smaller species investing more time in non-defensive behaviors compared to the larger species. More specifically, the smaller species *M. caroli* and *A. agrarius* allocated more time to exploration and foraging, whereas the larger rat species *R. exulans* and *R. losea* spent more time motionless or concealing. During the second trial, the addition of leopard cat cues did not elicit antipredator behaviors, but rather, rodents were found to exhibit increased non-defensive behaviors, specifically foraging efforts. The results suggest that these four species do largely follow a behavioral fast-slow continuum with the two smaller mice species demonstrating increased boldness in a novel context compared to the larger rat species. Also, the wild populations of rodents in eastern Taiwan may be naïve to leopard cats. Finally, the rodents in this study demonstrated habituation to the microenvironment, indicating they possess adaptive capacity.

**Keywords:** predation risk, behavior, rodent, foraging, novelty, leopard cat, defensive, fast-slow continuum

## Introduction

The pace-of-life (hereafter POL) hypothesis suggests that closely related species should differ in a suite of physiological (e.g. metabolic rate) and morphological (e.g. body size) traits that have coevolved with their respective life-histories in a fast-slow continuum (Stearns, 1983; Wikelski & Ricklefs, 2001; Ricklefs & Wikelski, 2002). It is well documented in mammals that small species embodying fast-paced life histories tend to favor current reproduction over survival since they are shorter lived, as opposed to larger slow-paced strategists with longer lifespans prioritizing survival over reproduction – thereby exemplifying the fast-slow continuum (Stearns, 1983; Dobson & Oli, 2004). A growing body of research has postulated that behavior is linked to POL (Sih et al., 2004; Réale et al., 2007; Stamps, 2007; Réale et al., 2010; Dammhahn et al., 2018). More specifically, species with fast life histories may also be more likely to express behaviors for increased boldness, fast exploration and foraging for resources, even at risk to their survival (Ricklefs & Wikelski, 2002; Montiglio et al., 2018; Royauté et al., 2018). Additionally, species with a slower POL are predicted to exercise more caution in response to risk (Wolf et al., 2007; Sol et al., 2018). Therefore, a comparative study investigating the behavioral responses of several species to risky contexts could provide a means of testing the links between POL and behavior.

An increasing number of studies have been devoted to animal personality, which can be defined as between-individual variation in behaviors that are consistent over time and across contexts (Sih et al., 2004; Réale et al., 2007; Carter et al., 2013). Among the personality trait axes defined [6], shyness-boldness, exploration-avoidance, and activity are commonly applied to risk-related studies (Martin & Réale, 2008; Dammhahn &

Almeling, 2012; Cremona et al., 2015; Mella et al., 2015). Behavioral types, or personality traits, have direct implications for fitness, since they can govern habitat use, social interactions, dispersal and responses to risk (Dall et al., 2004; Martin & Réale, 2008). Given that many species have been found to exhibit intra-individual consistencies and inter-individual variation for behaviors and habituation (Martin & Réale, 2008; Cremona et al., 2015; Mazzamuto et al., 2019) this is an important aspect to consider in a comparative study examining behavioral responses of multiple species to novelty.

Sexual variation in life history traits and subsequent dissimilarities in risk-taking behavior may also be expected for many species, particularly those with polygamous mating and/or female parental care (Trivers, 1972; Jolles et al., 2015). Therefore, in mating systems where the reproductive success of males may be more variable than females, the former sex may demonstrate more boldness, be more proactive in exploration of novel situations and more likely to take risks to acquire resources (Harris et al., 2010; King et al., 2013).

Studies manipulating predation risk have been executed in both laboratory and field settings and often use olfactory cues of predators (Bramley & Waas, 2001; Apfelbach et al., 2005; Apfelbach et al., 2015; Bedoya-Perez et al., 2019). Laboratory studies provide the ability to control for extraneous or unwanted factors, as well as the simulation of ‘micro-environments’ and observation of behaviors at a very fine scale. Risk-related laboratory experiments often involve rodents tested in a maze or open-arena and exposed to a stimulus, e.g. novel object, predator odor (Bedoya-Perez et al., 2019; Dielenberg & McGregor, 2001; Takahashi et al., 2005). Many studies performed on captive-reared rodents have found positive effects of predator odors; acting as deterrents (Apfelbach et

al., 2005; Takahashi et al., 2005). Other studies that have tested wild-caught rodents have found no effect of predator odor (Cremona et al., 2015; Apfelbach et al., 2005; Apfelbach et al., 2015; Kovacs et al., 2012; Stryjek et al., 2018). Wild rodents may not have the same behavioral responses as captive ones, especially since they have higher genetic variation promoting greater diversity of morphological and behavioral traits (Barnett, 2008; Dingemanse & Réale, 2013). Additional explanations for the inconsistencies in prey responses to predator odors include species traits, individual personality and differences, physiological state, and fear conditioning and habituation (Cremona et al., 2015; Bedoya-Perez et al., 2019).

Rodents are common prey to a suite of predators, and in order to keep pace in an evolutionary arms race they have been equipped with antipredator responses (Brown et al., 1999; Wolff & Sherman, 2008). Predator cues, such as odors, elevate risk for prey and can instigate defensive behaviors including increased vigilance, avoidance of areas, hiding, immobility and decreased activity (Apfelbach et al., 2015; Bytheway et al., 2013; Farnworth et al., 2019). These antipredator responses come at a cost, for example, according to the ‘predator sensitive foraging hypothesis’ the risk of predators will constrain prey foraging activity and efficiency due to an increase in defensive behaviors, such as vigilance and motionlessness (Wolff & Sherman, 2008; Creel & Christianson, 2009; Anson et al., 2013).

In Taiwan, a mammalian predator of rodents is the leopard cat (*Prionailurus bengalensis*) (Kerr 1972). Leopard cats, the sole-remaining native cat, are classified as endangered and protected under Taiwan’s Wildlife Conservation Act. This wild felid currently occupies a fraction of its once island-wide distribution (McCullough, 1974), which is limited to a few

regions in the western part of Taiwan where the sympatric rodents are a major constituent of the cat's diet (Chuang, 2012). The same murine rodent species are also distributed in eastern Taiwan, where leopard cats are no longer found. These rodents, which include both native and exotic species, vary in body size and associated life history traits (Adler, 1995; Kuo et al., 2011a); the larger rat species can be more than ten times the size of the smaller mice species. Additionally, the smaller mice species have shorter life spans and reach sexual maturity at an earlier age compared to the larger murid rats, as well as differences in fecundity and number of reproductive periods (Dobson & Oli, 2007; Yu & Lin, 1999; Qi, 2008). Therefore, despite occupying similar habitat, the various murid species in eastern Taiwan embody variation in their POL following a fast to slow continuum (Ricklefs & Wikelski, 2002; Réale et al., 2006), and may exhibit different strategies regarding exploration, acquisition of resources, and assessing risk. Furthermore, these differences in strategies may also be reflected in their behaviors; smaller species demonstrating more boldness in response to risky situations compared to the larger species (Sih et al., 2004; Réale et al., 2007; Royauté et al., 2018).

The Pacific rat (*Rattus exulans*) is one invasive species that has been expanding its range and invasion front in eastern Taiwan (I. Best, unpublished data). Invasive species that are widely distributed are generally thought to be generalists and ecologically plastic (Jones et al., 2008); in order to invade a diverse array of habitats. Furthermore, it has been posited that generalist species are more likely to confer boldness and less likely to express neophobia compared to specialist counterparts (Greenburg, 2003; Réale et al., 2010). Therefore, an invasive rat may respond differently than native species when exposed to a novel situation.

The present-day distribution of leopard cats and rodents allowed for testing the effects of cues from an allopatric predator on multiple rodent species. Since none of the rodents included in the study had ever encountered leopard cats, I could provide a first-step approach to evaluate whether these antipredator behavioral responses are conserved or lost rendering the rodents naïve. In this study, I conducted a laboratory experiment (Figure 2.1) on four wild rodent species in eastern Taiwan and measured their behavioral responses (Refer to Table 2.1 for a description of each behavior) to a novel environment and a novel predator cue (leopard cat odor). This experimental design also enabled the investigation of whether the rodents would habituate to novel conditions. Therefore, my objectives were to examine whether (1) there would be inter-sexual behavioral differences to the novel environment, (2) there would be inter-specific variation in behavioral responses to the novel environment and leopard cat odor, following a fast-slow continuum, (3) leopard cat odor would elicit defensive behaviors, and (4) rodents would become habituated to the experimental trials.

## Methods

### *Study area*

I conducted this study in Hualien County located in eastern Taiwan. The experiments took place at National Dong Hwa University, Shoufeng Township, Hualien County (23.90 °N, 121.54 °E). In low-elevation areas of Hualien a variety of habitats supports rodents including the Ryukyu mouse (*Mus caroli*), striped field mouse (*Apodemus agrarius*), lesser ricefield rat (*Rattus losea*), greater bandicoot rat (*Bandicota indica*), as well as the introduced species the house mouse (*Mus musculus*) and Pacific rat (*Rattus exulans*).

Leopard cats have been absent in Hualien for multiple decades, but there are historical records of their occurrence in the region (McCullough, 1974). This allowed me to test leopard cat odors as a novel predator cue and to assess whether the native rodents are naïve to leopard cat odors and subsequently lack anti-predator behavioral responses.

### ***Animal collection and maintenance***

Animals were live-trapped using a combination of Sherman (26.5 X 10 X 8.5 cm) and mesh (27 X 16 X 13 cm) traps. I deployed the traps at sites in fields of the agricultural areas of northern Hualien County. Since an objective of this study was to include individuals from multiple rodent species, I sampled different habitat types. All sites were a minimum distance of 500 m apart and only sampled once to ensure that the same individual was not trapped more than once. Wang & Wang (2001) reported that large rodent species, such as *R. losea*, rarely move more than 500 meters. Traps were baited with sweet potato covered in peanut butter and set in the late afternoon and rechecked first thing the next morning.

The target species included two mice species, *M. caroli* and *A. agrarius*, and two rat species, *R. exulans* and *R. losea*. The inclusion of these species was due to higher trapping success and for inter-specific representation of rodent communities exhibiting variation in morphological and life history traits. Additionally, since *R. exulans* is an invasive species (Kuo et al., 2011b), I wanted to determine if there were any associated behavioral differences from the other native species. Only adults of each species group were included in the experimental trials. Upon capture, target species that met the criteria were examined to determine sex and reproductive status. Reproductive maturity was concluded if testes were descended in the scrotal region for males, and the presence of vaginal perforation and/or swollen nipples for females. To avoid potential sources of behavioral bias, if females

were considered pregnant they were excluded from the trial. I also measured body weight ( $\pm 0.1$  g), body length (snout to anus, mm) and tail length (anus to tail tip, mm). Animals were kept for a maximum period of 48-hours after which they were released at the same site they were captured. I kept rodents in a designated housing room in mesh cages (27 X 16 X 13 cm); with one rodent housed per cage and no more than ten test animals were kept at a given time. Rodents were provided with water and food *ad libitum* until 10 hours before each trial. Additionally, cages contained shredded paper for bedding, a cardboard tube for hiding, and I placed a cover over all cages for additional privacy and to maintain separation. The housing room was maintained at  $24 \pm 1^\circ\text{C}$  with natural lighting. I was the only one to enter the housing room to provide water, food and to collect rodents for the trials; this was to minimize disturbance.

### ***Predator odor***

Leopard cat body odor and fecal samples were collected from captive individuals at Taipei Zoo and Pingtung Rescue Center for Endangered Wild Animals. Body odors were obtained by placing clean towels sterilized by an Autoclave in the sleeping areas of that cats' enclosures for a period of roughly 30 days. This duration was to allow for the towel to be sufficiently permeated with the leopard cat's odor. Upon receiving the towels, they were cut into smaller segments (15 X 15 cm), which has proven to be an effective size at eliciting antipredator behavioral responses in prey species (Takahashi et al., 2005; Garvey et al., 2017). The segments were then placed in airtight, re-sealable plastic bags and stored in a  $-20^\circ\text{C}$  freezer until later use. Clean, latex gloves were worn at all times when handling the towels. Fecal samples were also collected from the same donor individuals that provided the body odor samples. Upon request of collection, fresh feces were collected

daily, placed in airtight, re-sealable plastic bags and stored in a freezer at -20 °C. Samples were stored in a freezer for a maximum period of two months before use. On the day of experimental trials, fecal samples of the same donor individual were thawed and pooled together. The feces were then crushed and diluted with distilled water to create a mixture with a ratio of 1-part feces (g) and 1-part distilled water (mL). This ratio has been commonly used in other predator odor experiments (Apfelbach et al., 2005; Navarro-Castilla et al., 2014). I used body odor and fecal samples in concert for the leopard cat odor treatment. Corresponding body odor and fecal samples of the same donor individual were always paired together. I did not consider the combination of both odor types to be an exaggeration of leopard cat cues, since my aim was to simulate high predation risk. Furthermore, predators, such as felids, often leave multiple scent types at areas they visit (Hunter & Barrett, 2015; Jones et al., 2016; Moll et al., 2017).

### ***Experimental apparatus***

Trials were conducted in an open-area test arena (165 cm long X 80 cm wide X 70 cm deep; Figure 2.1), which consisted of an opaque, rectangular-shaped box made of plastic material that was non-permeable and easy to clean. The size of the arena was to allow for sufficient exploration and to prevent escape. The arena was divided into three-sections using a non-odorous tape that was clearly visible under low light; in section 1 a PVC tri-entry tube (referred to as the hide; 50 mm diameter) was placed in the center to allow concealing. I thought it was important to include a hide, as evasion and/ or hiding are common defensive behavioral responses of wild rodents when facing risk (Wolff & Sherman, 2008; Blanchard et al., 2005). In section 3 at the opposite end of arena I placed a foraging tray and the treatment apparatus (present only during the treatment trial) (Figure

2.1). The foraging trays (17.3 X 12.1 X 3.8 cm) contained 5.0 g of millet seed mixed thoroughly in 75 g of extra fine sand. Through my preliminary tests and pilot study, I was able to determine millet seed as an appropriate food source. The purpose of including the foraging tray was to assess propensity to forage in a novel environment and risky context, which enabled a metric for boldness to be measured (Dammhahn & Almeling, 2012; Mella et al., 2015; Toscano et al., 2016).

I affixed a WI-FI enabled surveillance camera (D-Link DCS-936L; D-Link, Taipei, Taiwan) equipped with infrared capabilities to the upper edge of the interior wall above section 3 (Figure 2.1) and positioned the camera to fit the treatment apparatus, foraging tray and hide in the field of view. This camera also provided live streaming of all trials. I also used a camcorder (HausBell HDV-302S; USCLOUD Trade Inc., California, USA) with infrared attached to a tripod and positioned to have the interior of the arena in the field of view. The combination of the two cameras ensured there were no blind spots and the whole interior of the arena was fully captured.

The apparatus for the leopard cat odor treatment consisted of a body odor towel segment placed on a tray (22 X 17 X 3 cm) with 5 g of the fecal solution on a petri dish positioned on top. The non-odor control treatment comprised a clean towel segment sprayed with distilled water placed on a tray with an empty petri dish on top. These apparatus are hereafter referred to as treatment apparatus.

### ***Trial procedures***

The experimental trials took place from September to November 2018 and January to June 2019. All trials were conducted between 18:00 and 23:00, starting after dusk, in a testing room with the lights turned off to reflect natural light conditions and account for

the rodents' active period. Test subjects were food deprived for at least 10 hours before each trial since an objective of this study was to examine foraging behavior. All test animals were tested for two consecutive nights. The purpose of the first trial (first night for each animal) was to test the rodents' responses to a novel environment (test arena), therefore the treatment apparatus was excluded. During the second trial on the successive night, which included the treatment apparatus, the main aim was to assess the rodents' responses to the predator odor. The order for animals to be tested was randomly selected and kept the same upon the second night to allow for 24 hours between each animal's trials. Test animals were transferred to the testing room in their cages for each of their trials. The cages were placed in section 1 (Figure 2.1) of the test arena and their cage door was left open. Once it was confirmed that the rodent had left their cage and entered the arena, cages were removed, cameras were activated, and I exited the testing room. Trials were able to be viewed from a separate room via a live stream of the surveillance camera, in addition to being video recorded. The duration of all trials was 35 minutes, which included a 5-minute introductory period, followed by a brief disturbance (placement of treatment apparatus in the arena), then the remaining 30 minutes. I selected this length for the trials since my aim was to measure immediate responses to a novel environment and predator cue. Similar trial durations and inter-test intervals have been employed in lab-based predator odor experiments that have tested on rodents (Apfelbach et al., 2005; Takahashi et al., 2005; Hegab et al., 2014; Storsberg et al., 2018). During the first trial, since the treatment apparatus was absent and not placed in the arena, I mimicked the procedure of entering the testing room after the 5-minute introductory period to control for any effects on behavior that the disturbance (placement of treatment apparatus) in the second trial would cause.

During the second trial, the treatment apparatus was placed in section 3 of the arena adjacent to the foraging tray (Figure 2.1). Upon completion of each trial, animals were returned to their cages and housing room. The remaining food content in the foraging trays were sieved and weighed using an electronic scale ( $\pm 0.1$  g) before replacing the seeds and sand. I thoroughly cleaned the test arena and apparatus using 75% ethanol and allowed at least 30 minutes for any lingering odors in the testing room to dissipate before starting the next trial.

### ***Test subjects***

The sample from the experimental trials included 68 test subjects: 13 *M. caroli* (5 male, 8 female; average weight: male =  $12.8 \pm 0.7$  g, female =  $12.6 \pm 0.5$  g), 16 *A. agrarius* (7 male, 9 female; average weight: male =  $27.7 \pm 1.8$  g, female =  $28.2 \pm 1.0$  g), 22 *R. exulans* (15 male, 7 female; average weight : male =  $44.4 \pm 1.4$  g, female =  $33.1 \pm 1.6$  g), and 17 *R. losea* (10 male, 7 female; average weight: male =  $120.4 \pm 6.5$  g, female =  $109.4 \pm 5.7$  g). I employed a stratified random sampling design to assign a similar number of individuals from each species to either the control group or leopard cat odor group. Each treatment group consisted of 34 rodents (control = 7 *M. caroli*, 8 *A. agrarius*, 11 *R. exulans*, 8 *R. losea*; leopard cat odor = 6, 8, 11, 9, respectively).

### ***Behavioral response analysis***

The videos of all trials were analyzed manually offline and in-depth. The behaviors I scored were *exploring*, *foraging*, *motionless*, *concealing*, *grooming*, *consumption*, *foraging events*, *latency to forage*, *jumping* and *contact* (Table 2.1).

For each behavior to be considered and scored it would have to last for at least 3 seconds. I included the ‘head out’ behavior as part of *concealing* because it was not commonly

observed amongst the test subjects. Vigilant rearing was also not observed in the trials. Based on the preliminary trials, the test subjects did not display any preference for the different sections of the arena, so the time spent in different sections was not included. I further divided four of the five duration-based behaviors (Table 2.1) into two categories *defensive* and *non-defensive* defined as exhibiting *motionless* and *concealing*, and *exploring* and *foraging*, respectively. Exploration and foraging are commonly classified as non-defensive behaviors for rodents, whereas motionless and concealing are considered defensive responses to risk (Stryjek et al., 2018; Blanchard & Blanchard, 1989; McGregor et al., 2002). I defined these behavioral categories in order to test my prediction of inter-specific behavioral variation following a fast-slow continuum. *Contact* was only scored during the second trial because the treatment apparatus was absent in the arena for the first trial. *Consumption* was expected to vary across species in the experiment due to the inter-specific size disparity. To account for this, I calculated a *consumption ratio* defined as the amount of food eaten proportional to the animal's body weight and expressed as a percentage.

I found some of the measured behaviors to be highly correlated; time *exploring* with *jumping*, and time *foraging* with *consumption ratio* and *foraging events* based on Spearman rank correlations (Table S2.1). Additionally, *latency to forage* was significantly negatively correlated with time *foraging* (Table S2.1). To avoid redundancy, I excluded the behaviors *consumption ratio*, *foraging events*, *latency to forage* and *jumping* from the focus and analysis included in the main text. Results of these behaviors are available in the Supplementary material (Table S2.4). Therefore, time spent *exploring* served as a proxy for exploration and activity (Sih et al., 2004; Réale et al., 2007; Berger-Tai et al., 2014),

and time *foraging* for resource acquisition and boldness (Dammhahn & Almeling, 2012; Mella et al., 2015).

### *Statistical analysis*

Since the response variables did not meet the assumptions of normality I employed generalized linear models (GLM) and generalized estimating equation (GEE) models encompassing various link functions that best fit the distribution of the data. For longitudinal analysis, GEEs have been found to be very robust, flexible and well-suited models for behavioral data that violate the assumptions of normality (Pekár & Brabec, 2018). To take into account potential seasonal influences on rodent behavior, I initially included a seasonality variable in the models; defined as the difference in days between a baseline date (July 1<sup>st</sup> 2018) and the date of the trials. This seasonality variable had no significant effects on any of the behavioral responses, so I excluded it from all successive models to not exhaust too many degrees of freedom. Additionally, because species already considers differences in life history and morphological traits, such as size, I did not include body weight as a factor in the models.

To test responses to a novel environment (first trial only), for all the duration-based response variables, with the exception of *exploring* and *non-defensive* behaviors, I ran a GLM incorporating a negative binomial log-link function with a fixed offset value equal to 2100 (total amount of time in seconds in a trial). In these models, the predictors were fixed factors species and sex, as well as their interaction. The response variables *exploring* and *non-defensive* were analyzed using a GLM fit with a gamma log-link function; with species and sex set as the fixed factors.

I measured rodent responses to leopard cat odor using a GEE (with the exception of *contact*) with test animal ID as the subject variable and trial as the within-subject variable. GEEs with negative binomial log-link functions were performed for each duration-based response incorporating an offset equal to 2100 and setting trial (first and second), treatment (leopard cat odor or control), and species as the fixed factors. The variable trial was included in the models as a factor because in addition to testing the effects of a predator odor, I sought to assess any differences in behaviors between the first and second trials. I included two-way interactions between the fixed factors in the models, but not a three-way interaction. I excluded a three-way interaction because it did not coincide with my research objectives and to save degrees of freedom. The variable sex was excluded from these models since animal ID was already included, which factored in sex as well as the other unique characteristics of an individual animal. Additionally, testing the effect of sex was not an objective for the second trial. For the response *contact* I ran a GLM with a negative binomial log-link function and included treatment and species as fixed factors, since this variable was only measured during the second trial. Post hoc analyses were performed for all models to test for differences between subgroups (e.g. species groups, trials of a species) of the fixed factors using estimated marginal means with a pairwise contrast incorporating a least significant difference.

In order to assess the potential importance of within-individual consistency for the measured behaviors (Martin & Réale, 2008; Carter et al., 2013; Cremona et al., 2015; Dingemanse & Dochtermann, 2013), I performed two comparisons of linear mixed models (LMMs) with the restricted maximum likelihood (REML) method; each comprising two models. In the first comparison, one model only included intercept, and the second model

included intercept and rodent identity (ID) set as a random effect. This model provided a baseline for amount of variance explained by rodent ID (Table S2.5). In the second comparison, both models included species, trial and treatment as fixed effects, and only one model included ID as a random effect. For each comparison, the two models (with or without ID as a random effect) were tested for significance of between-individual variance of a behavior by calculating the log-likelihood ratio (Martin & Réale, 2008; Cremona et al., 2015; Dingemans & Doehrmann, 2013). I approximated the  $p$ -value of the log-likelihood ratio test (LRT) following Martin & Réale (2008). For each behavior, repeatability was estimated as  $R = V_i / (V_i + V_r)$ ; where  $V_i$  is the variance of the random effect (rodent identity) and  $V_r$  is the residual variance (Dingemans & Doehrmann, 2013; Mazzamuto et al., 2019). Please refer to the Supplementary material for the results (Table S2.5 and S2.6).

For all of the statistical analyses significance was considered at  $\alpha = 0.05$ . All statistical analyses were performed with SPSS v.25.0 (IBM, Armonk, USA).

## Results

### *Behavioral responses to a novel environment*

The analysis found significant effects of species for all behavioral responses (Table 2.2, Figure 2.2). The two mice species, *M. caroli* and *A. agrarius*, spent more time performing non-defensive behaviors, whereas the two rat species, *R. exulans* and *R. losea*, invested more time in defensive behaviors during the first trial (Figure 2.2A). Furthermore, during the first trial the species *M. caroli* spent the most time exploring, while *A. agrarius* spent

the most time foraging (Figure 2.2B). *R. losea* spent more time motionless and grooming compared to the other species, and *R. exulans* spent the most time concealing (Figure 2.2B).

Sex had significant effects for the responses *foraging*, *concealing* and the *non-defensive* behavioral category; with significant interactions of sex and species for *foraging*, *motionless*, *concealing*, and *non-defensive* (Table 2.1). The males of all species combined spent more time exhibiting non-defensive behaviors, specifically foraging, whereas females spent more time concealing. At the species level, males of *R. losea* invested significantly more time foraging compared to females (both  $P < 0.005$ ). Additionally, females of *R. losea* spent more time concealing in the hide ( $P < 0.05$ ). Despite the absence of significant differences, I observed a trend of the males of each species group allocating slightly more time to foraging; as well as the females of *M. caroli* and *A. agrarius* staying concealed for marginally longer durations (Table S2.2). Females of the species *R. exulans* spent more time motionless compared to males ( $P < 0.05$ ).

### ***Behavioral responses to leopard cat odor***

Leopard cat odor was found to have no significant effect on the *non-defensive* behavioral category (Table 2.3). There was a significant interaction between species and treatment for the *defensive* behavioral category, but not *non-defensive* (Table 2.3). More specifically, the leopard cat odor treatment group of the species *A. agrarius* spent more time exhibiting defensive behaviors compared to the control group (Figure 2.3A).

For both behavioral categories there were significant differences between species (Table 2.3). The two mice species *M. caroli* and *A. agrarius* spent less time exhibiting defensive behaviors and more time performing non-defensive behaviors compared to the larger rat species, *R. exulans* and *R. losea* (Defensive: *M. caroli* compared to *R. exulans* and *R. losea*,

both  $P < 0.005$ ; *A. agrarius* compared to *R. exulans* and *R. losea*, both  $P < 0.001$ ; Non-defensive: *M. caroli* compared to *R. exulans* and *R. losea*, both  $P < 0.005$ ; *A. agrarius* compared *R. exulans* and *R. losea*, both  $P < 0.05$ ).

Leopard cat odor had significant effects on *concealing* for *A. agrarius* and *motionless* for *R. exulans*. *A. agrarius* exposed to the predator odor spent more time concealing than their counterparts without exposure (Figure 2.4D). These results may be explained by within-individual consistency in concealing behavior across the two trials for two individuals of *A. agrarius* (1 male, 1 female) that were included in the leopard cat odor treatment group (Table S2.5, S2.6). These two individuals were also outside the upper 95% confidence interval for the mean of time spent concealing. The control group of the species *R. exulans* spent more time motionless compared to the group exposed to leopard cat odor (Figure 2.4C). These results may not be so much of an effect of the leopard cat odor, but rather between-individual variation for the behavior (Table S2.5, S2.6).

Leopard cat odor did not discourage rodents from making contact with the treatment apparatus (Wald  $\chi^2 = 0.04$ ,  $P = 0.85$ ), nor was there an interaction between treatment type and species for this behavior (Wald  $\chi^2 = 0.55$ ,  $P = 0.91$ ). There were significant differences between species for the behavior *contact* (Wald  $\chi^2 = 7.98$ ,  $P < 0.05$ ; Figure S2.2). *M. caroli* had the highest number of contacts, irrespective of treatment type (*M. caroli* compared to *A. agrarius*, *R. exulans* and *R. losea*, all  $P < 0.05$ ).

### ***Behavioral responses across trials***

The amount of time each species group exhibited *defensive* or *non-defensive* behaviors did not differ significantly between trials (Table 2.3). However, trial had significant and

species-specific effects on the behaviors *exploring*, *foraging*, *motionless* and *grooming* (Table 2.3).

With the results of both treatment groups (control and leopard cat odor) in the second trial combined, *A. agrarius* displayed a decrease in time spent exploring on the second night (Figure 2.4A), and both *A. agrarius* and *R. exulans* significantly increased the time spent foraging (Figure 2.4B). Also, during the second trial the species *R. exulans* and *M. caroli* reduced the amount of time spent motionless (Figure 2.4C), and *R. exulans* and *R. losea* spent significantly less time grooming (Figure 2.4D).

### ***Intra-individual consistency of behaviors***

Based on the analysis of repeatability, rodent ID had significant effects for all behaviors except *grooming* for the first conditional model (without fixed effects; Table S2.5); and significant effects for all behaviors except *exploring* and *grooming* for the second conditional model (with fixed effects; Table S2.6). These results suggest that for most behaviors there was within-individual consistency (repeatability) and between-individual variation (Table S2.5, S2.6).

## **Discussion**

In the present study, inter-specific variation was observed for behavioral responses in an experiment testing novelty. On average, the smallest species in my sample, *M. caroli*, spent the most time exhibiting non-defensive behaviors, predominantly comprised of exploring. The other mouse species and second smallest, *A. agrarius*, spent the most time foraging. Contrarily, the two rat species in the experiments spent considerably more time demonstrating defensive behaviors; *R. exulans* spent the most time hiding and *R. losea* was

motionless for the longest cumulative period. *R. losea* also spent the most time grooming during the first trial, which could reflect nervousness or be a reaction to a stressor (Kalueff et al., 2007; Martin & Réale, 2008), such as the novel environment. In addition to being larger, the rat species, included in the present study, have longer lifespans and reach sexual maturity later compared to the two mice species (Qi, 2008). These results suggest that the different species fit a fast-slow continuum with predicted associated behaviors (Réale et al., 2007; Stamps, 2007; Réale et al., 2010; Dammhahn et al., 2018), demonstrated in the present study by the smaller mice species performing a higher proportion of riskier behaviors (exploration, activity and foraging) in a novel situation, in contrast to the larger rat species. The smaller species in this study, *M. caroli* and *A. agrarius*, prioritized fast exploration or acquisition of resources, as oppose to defensive behaviors. *A. agrarius* favored the acquisition of resources over exploration or cautious behavior in an unfamiliar situation. These results may indicate a trade-off favoring current fitness returns compared to future expectations (Montiglio et al., 2018; Wolf et al., 2007). Similarly, Vasquez (1996) studying foraging behavior of three different Chilean rodent species varying in body size found that under increased risk the largest species was the most cautious.

The response variables foraging and concealing were found to differ significantly between sexes. At the rodent community level (all species combined), males spent more time foraging compared to females for their first trial. Since male rodents generally have less parental investment and are promiscuous, it can be expected that there will be sex-related differences for trade-offs between risk and reward (Trivers, 1972; Wolff & Sherman, 2008). Therefore, males may have a higher propensity to expose themselves to risk in return for a reward (Jolles et al., 2015); in the case of the present study, risk of

exposure in an unfamiliar environment and a reward of access to food. Male rodents are generally larger than females (Wolff & Sherman, 2008; Wilson et al., 2017), therefore, they may also have a higher food intake potential (Fukushima et al., 2015), as was observed in the present study. Overall, the defensive behavior concealing was higher for females, which indicates that in response to a novel, unfamiliar situation females exercised more caution. Adult, sexually mature females may show a preference for defensive behaviors in a novel context since the risks may outweigh rewards as they incur higher costs for parental care (Wolff & Sherman, 2008; Wilson et al., 2017). These results are consistent with other studies examining behavioral responses to high risk situations (Bramley & Waas, 2001; Jolles et al., 2015), with female rodents exhibiting a higher proportion of defensive behaviors, such as hiding, compared to males.

The presence of leopard cat cues during the second trial did not have effects on the defensive and non-defensive behavioral categories. There was, however, species-specific significant effects (increased concealing in *A. agrarius* and decreased motionlessness in *R. exulans* in response to leopard cat odor), which can most likely be attributed to within-individual consistency and between-individual variation. Individuals of *A. agrarius* that were assigned to the leopard cat odor treatment group also were more inclined to hide, which was observed consistently over both trials. Between-individual variation could explain how individuals of *R. exulans* in the control group spent more time motionless during the second trial compared to those in the predator odor group. Repeatability of behaviors over time and even across varying situations has been observed in similar experiments (Martin & Réale, 2008; Schuster et al., 2017; Uchida et al., 2020), and can even outweigh the effects of predator odors (Cremona et al., 2015).

The predator odor failing to elicit aversive behaviors in the present study conforms with many other studies that have exposed rodent species from wild populations to predator cues both in lab (Cremona et al., 2015; Bramley & Waas, 2001; Jolly et al., 2018) and field (Powell & Banks, 2004; Shapira et al., 2013; Stryjek et al., 2018) contexts. Furthermore, many studies that have found significant effects of predator odors performed their experiments on captive-bred rodents (Apfelbach et al., 2005; Hegab et al., 2014; Jolles et al., 2015; Storsberg et al. 2018). The domestication process of captive rodents may lead to an inhibition of behavioral variation and adaptability (Price, 1984; Barnett, 2008), resulting in more pronounced responses to foreign odorous stimuli. There is a growing consensus stipulating that for wild prey populations predator odors alone may not evoke strong antipredator responses (Orrock et al., 2004; Réale et al., 2007; Stryjek et al., 2018), but in turn, a combination of factors, including physiology, type of perceived risk, and habituation (Bedoya-Perez et al., 2019). Indirect risk factors, such as illumination and vegetation cover, have been found to play larger roles in governing rodent foraging behavior compared to direct predator cues, such as odor (Orrock et al., 2004; Crego et al., 2018; Farnworth et al., 2019).

Since leopard cats have been absent in eastern Taiwan for several decades, and therefore numerous generations of the local rodent species, it is possible these respective rodents have lost the ability to discriminate the odor. Additionally, other small carnivores in eastern Taiwan that are capable of predating on rodents, such as the lesser civet (*Viverricula indica*) and feral cats (*Felis catus*), occur at low densities (I. Best, unpublished data) or rodents are not a main prey item for them (Chuang & Lee, 1997; Hunter & Barrett, 2011). Antipredator responses are very costly (Blumstein & Daniel, 2005) and if a given trait no

longer serves a purpose it is likely that it will be selected against and lost (Lahti et al., 2009). Furthermore, according to the naiveté hypothesis prey are not expected to discriminate and respond accordingly to novel predators due to no previous encounters (Carthey & Blumstein, 2018). In Australia, the invasion of cane toads (*Rhinella marina*) prompted the relocation of native Northern quolls (*Dasyurus hallucatus*) to predator-free islands, and they have lived in these conditions for multiple generations (Jolly et al., 2018). Jolly et al. (2018) compared responses of quolls from both the predator-free island population and mainland Australia to native predator cues. Opposite to the mainland quolls, the island population showed no aversion to the predator odors. For the current study, despite the possibility that rodents inhabiting leopard cat-free regions are naïve to the predator and are unable to recognize their odors, further research testing rodents in areas where leopard cats are present is necessary to affirm this prediction.

Given the lack of predator odor effects on rodent behavior, I was able to examine behavioral responses across trials. Two out of the four species showed significant increases in amount of time foraging, and *M. caroli* did spend more time foraging despite the difference not being significant. *M. caroli* and *R. exulans* also significantly decreased the amount of time spent motionless during the second trial. Therefore, the three species, *M. caroli*, *A. agrarius* and *R. exulans*, demonstrated a trade-off in defensive behaviors, as well as exploration, for access to food resources, which can be indicative of boldness (Réale et al., 2007; Dammhahn & Almeling, 2012; Mella et al., 2015). Even though exploring can be constituted as a non-defensive behavior conferring some boldness (Sih et al., 2004; Patrick et al., 2017), individuals are still able to keep some level of vigilance (Réale et al.,

2007; Montiglio et al., 2018) whereas with foraging, vigilance is sacrificed to a much higher degree (Lima & Bednekoff, 1999).

The results of this study provide further support that wild populations of rodent species can have behavioral plasticity, as habituation can be linked to phenotypic plasticity (Martin & Réale, 2008; Rodríguez-Prieto et al., 2011). In the case of the present study, the increase in foraging activities and exploitation of the food patch can reflect learning and be a measure for information processing (Elliot & Grunberg, 2005). Moreover, after accumulating sufficient knowledge of an initially unfamiliar environment (through repeated exposure), an optimal strategy could be to switch from exploration to exploitation of resources for an energetic reward (Berger-Tai et al., 2014; Patrick et al., 2017). Additionally, the variation between individuals that was observed in the experiments (Table S2.5 and S2.6) could also indicate large behavioral repertoires of the wild populations (Shettleworth, 2001). Therefore, the behavioral differences did not stop at the species level, but also within species at the individual level. A broad behavioral repertoire could also have implications for fitness under a changing environment – increased human activity and disturbance. A species with a wider behavioral range (boldness-shyness) may be more resilient to disturbances (Réale et al., 2010; Beever et al., 2017).

I find it unlikely that the increases in foraging activity observed were stress-induced or a product of the experimental procedure. Animals were food deprived for the same amount of time on both days of testing and were provided with ample food upon return to their housing cage after completing the first trial. Moreover, high levels of acute stress on rodents may inhibit food intake and prompt defensive behaviors (Calvez et al., 2011; Ulrich-Lai et al., 2015). I also consider it unlikely that the addition of novel objects

(treatment apparatus) during the second trial masked the effects of the predator odor by instigating strong neophobic responses, since a majority of the test animals displayed the opposite response indicated by a decrease in defensive behaviors and exploration, irrespective of treatment type.

Although the results of this study demonstrate changes in behavior across trial and context, likely reflecting habituation, I acknowledge that the short inter-trial interval may have influenced this result. Since a main objective of this study was to test the immediate responses of wild-caught rodents to a novel environment and predator odor, my experimental design did not incorporate lengthy intervals between testing. Additionally, many predator odor studies have used similar experimental durations and intervals (Takahashi et al., 2005; Hegab et al., 2014; Cremona et al., 2015; Storsberg et al., 2018). This study does provide a first-step approach for evaluating inter-specific habituation to a microenvironment in a controlled setting for the included species. To further substantiate these results, future studies could adopt a longer period between testing and incorporate repeated measures that more appropriately fit the research questions.

The largest species included in this study, *R. losea*, had contrasting responses compared to the other species during the second trial. Namely, the species failed to exhibit significant increases in any of the non-defensive behaviors. The species did decrease the amount of time grooming, however, possibly suggesting a decrease in reactionary stress (Kalueff et al., 2007). The former results may indicate different rates of habituation between the species. On average, *R. losea* ranged from three to ten times larger in size than the other species. With the predictions of the POL following a behavioral fast-slow continuum (Wolf et al., 2007; Réale et al., 2007; Réale et al., 2010), *R. losea* would be expected to be the

most cautious species in the study, therefore, it could also be possible that this species would habituate to novelty at a slower pace. Larger species with slower life history traits tend to be more cautious with stronger neophobia responses (Dobson & Oli, 2007; Réale et al., 2010; Montiglio et al., 2018), therefore habituation to a novel situation with associated risk may be slower compared to smaller species.

The invasive species, *R. exulans*, somewhat surprisingly spent the most time concealing during the first trial. However, the second trial for this species comprised a drastic reduction staying motionless with an increase in foraging. The average amount of time spent hiding was also lower, though the difference between the two trials was not significant. These results demonstrate the plasticity and habituation potential of the rat, which may be characteristic of an invasive species (Sih et al., 2004; Wright et al., 2010; Harper & Bunbury, 2015). Additionally, the initial caution the species exercised could also be somewhat indicative of their strategy for occupying novel environments – not overly bold to a degree of recklessness. The species could benefit from processing information and assessing risk about the new environment from a safe refuge in addition to exploration (Chapple et al., 2011; Chapple et al., 2012). To better understand the habituation potential and rate of invasive species, further studies adopting a comparative approach involving multiple invasive and native species will be necessary.

Interestingly, in tandem with the range expansion of *R. exulans* in eastern Taiwan, *A. agrarius* has been experiencing population declines (Kuo et al., 2011b; I.N. Best, unpublished data). In the present study, I observed *A. agrarius* to be the most voracious foragers exposing themselves to risk for the longest periods of time. The lack of defensive behaviors to the simulated cues of risk in the experiments (novel environment and objects)

may suggest that they have an increased vulnerability to predators, biological enemies and other disturbances in the wild.

The assessment testing intra-individual consistency found most of the measured behaviors to be repeatable, supporting between-individual variation and likely behavioral types. Individuals in the trials fit a spectrum of boldness and exploration/ activity. Some caution should be exercised in the interpretation and application of these results due to the experimental design of this study. An initial aim of mine was to test inter-specific behavioral responses to a predator cue, therefore, the necessary addition of the treatment apparatus during the second trial changed a context parameter, which may impede validity and statistical power of repeatability tests (Dingemanse & Dochtermann, 2013). Despite this limitation, this comparative, exploratory study does provide a foundation for inter-individual variation and within-individual repeatability of behaviors on a multi-species level. I suggest that future studies employ the appropriate methodology and design better suited to examine personality traits of individuals amongst different species to advance understanding of behavioral plasticity in ecological contexts.

## **Conclusions**

Most studies to date examining behavioral and life history covariation have largely focused on individuals or populations of a single species (Réale et al., 2007; Le Galliard et al., 2013; Dammhahn et al., 2018), therefore this pioneer study provides further insight for the association between behavior and POL, exemplified by inter-specific behavioral variation in accordance with a fast-slow continuum. In a novel microenvironment, the smaller, “faster” species of mice displayed more proactive behaviors conferring boldness,

whereas the larger, “slower” rat species exercised more caution. The findings of this study also suggest that these four species of rodents in eastern Taiwan may be naïve to leopard cat cues, indicating that antipredator behaviors may be learned from experience. However, further research is required to uncover this assumption. Finally, despite the addition of a predator odor and novel object, I observed a trend for an increase in non-defensive behaviors across all species – representing habituation and behavioral plasticity. In the context of regions undergoing landscape changes facilitated by increased human activity and development, as is the case in Hualien County in eastern Taiwan, the survival and success of wild rodents may be dependent on broad behavioral repertoires.



## Tables

**Table 2.1.** Behavioral response variables measured from experimental trials

Response	Unit measured	Definition
<i>Exploring<sup>a</sup></i>	Time (s.)	Locomotive activity, investigation of the arena and objects, climbing
<i>Foraging<sup>a</sup></i>	Time (s.)	The subject consumed and/ or searched for seeds in the foraging tray
<i>Motionless<sup>b</sup></i>	Time (s.)	The subject remained stationary (except for breathing); body remained stationary with occasional head scanning
<i>Concealing<sup>b</sup></i>	Time (s.)	The subject was in the hide (at least 75% of the body was concealed); the head was slightly exposed from the hide
<i>Grooming</i>	Time (s.)	The subject was grooming, e.g. licking or rubbing
<i>Consumption<sup>c*</sup></i>	Weight (g)	The amount of seeds consumed ( $\pm 0.1$ g). Calculated by subtracting the remaining amount from the initial 5.0 g
<i>Foraging events<sup>*</sup></i>	No. occurrences	The number of events of foraging of the test subject
<i>Latency to forage<sup>*</sup></i>	Time (s.)	The amount of time before the subject started foraging
<i>Jumping<sup>*</sup></i>	No. occurrences	The subject actively jumped; all four paws left the base of the arena
<i>Contact</i>	No. occurrences	The subject investigated or had tactile contact with the treatment apparatus, e.g. sniffing or biting

Notes: seconds (s.), number of (no.) occurrences, grams (g). Response variables adapted from Dielenberg & McGregor, 2001; Hegab et al., 2014; Storsberg et al., 2018. <sup>a</sup> refers to behaviors included in the ‘Non-defensive’ behavioral category. <sup>b</sup> refers to behaviors included in the ‘Defensive’ behavioral category. <sup>c</sup> this behavior was transformed to *Consumption ratio*, by calculating the food eaten proportional to body weight and expressed as a percentage. \* indicates behaviors removed from the focus of the main text, see Supplementary material (Table S2.4, Figure S2.1, Figure S2.2) for results. For a complete list of the means and standard errors of all the response variables, please refer to Supplementary material (Table S2.2 and S2.3).

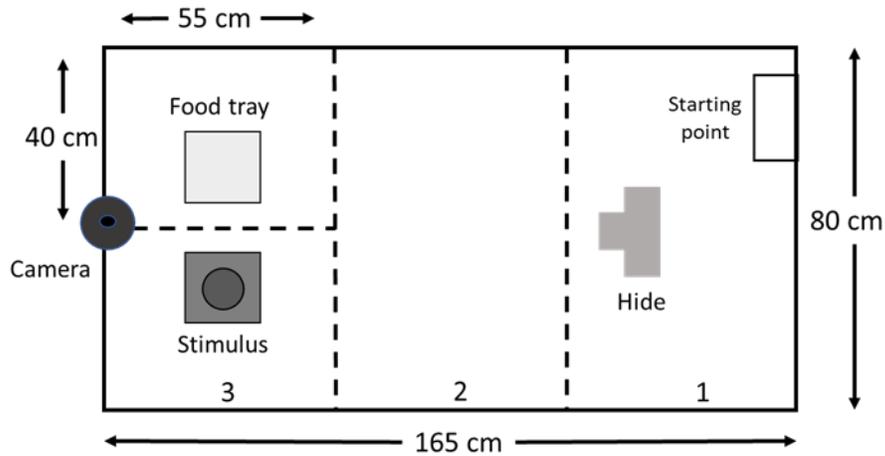
**Table 2.2.** Behavioral responses of the first trial for the factor species, sex and their interaction. Significant values are displayed in bold.

<b>Response</b>	<b>Factor</b>	<b>Wald <math>\chi^2</math></b>	<b>df</b>	<b>P</b>
<i>Defensive</i>	Species	19.03	3	<b>&lt;0.001</b>
	Sex	1.90	1	0.168
	Species $\times$ Sex	4.90	3	0.179
<i>Non-defensive</i>	Species	22.07	3	<b>&lt;0.001</b>
	Sex	4.86	1	<b>&lt;0.05</b>
	Species $\times$ Sex	11.80	3	<b>&lt;0.01</b>
<i>Exploring</i>	Species	38.90	3	<b>&lt;0.001</b>
	Sex	0.62	1	0.433
	Species $\times$ Sex	2.26	3	0.521
<i>Foraging</i>	Species	38.55	3	<b>&lt;0.001</b>
	Sex	24.68	1	<b>&lt;0.001</b>
	Species $\times$ Sex	30.55	3	<b>&lt;0.001</b>
<i>Motionless</i>	Species	48.77	3	<b>&lt;0.001</b>
	Sex	0.94	1	0.332
	Species $\times$ Sex	27.92	3	<b>&lt;0.001</b>
<i>Concealing</i>	Species	57.99	3	<b>&lt;0.001</b>
	Sex	29.28	1	<b>&lt;0.001</b>
	Species $\times$ Sex	41.71	3	<b>&lt;0.001</b>
<i>Grooming</i>	Species	32.14	3	<b>&lt;0.001</b>
	Sex	3.50	1	0.061
	Species $\times$ Sex	6.86	3	0.076

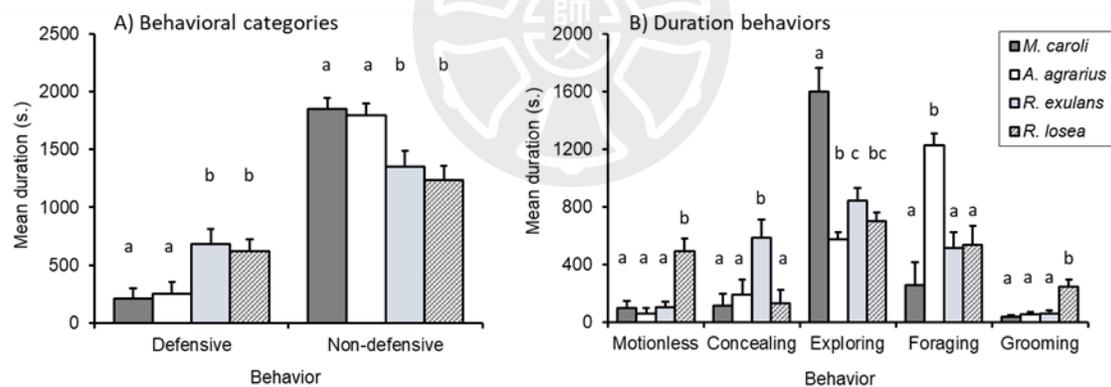
**Table 2.3.** Behavioral responses for the effects and interactions of trial, treatment and species. Significant values are displayed in bold.

<b>Response</b>	<b>Factor</b>	<b>Wald <math>\chi^2</math></b>	<b>df</b>	<b>P</b>
<i>Defensive</i>	Trial	0.06	1	0.800
	Treatment	1.99	1	0.159
	Species	51.57	3	<b>&lt;0.001</b>
	Trial $\times$ Treatment	0.06	1	0.810
	Trial $\times$ Species	4.63	3	0.201
	Treatment $\times$ Species	35.70	3	<b>&lt;0.001</b>
<i>Non-defensive</i>	Trial	2.46	1	0.117
	Treatment	0.27	1	0.603
	Species	22.67	3	<b>&lt;0.001</b>
	Trial $\times$ Treatment	0.01	1	0.979
	Trial $\times$ Species	3.23	3	0.358
	Treatment $\times$ Species	6.15	3	0.104
<i>Exploring</i>	Trial	12.18	1	<b>&lt;0.001</b>
	Treatment	0.39	1	0.531
	Species	155.08	3	<b>&lt;0.001</b>
	Trial $\times$ Treatment	0.02	1	0.882
	Trial $\times$ Species	24.71	3	<b>&lt;0.001</b>
	Treatment $\times$ Species	1.63	3	0.653
<i>Foraging</i>	Trial	4.96	1	<b>&lt;0.05</b>
	Treatment	0.10	1	0.756
	Species	42.90	3	<b>&lt;0.001</b>
	Trial $\times$ Treatment	1.27	1	0.261
	Trial $\times$ Species	11.86	3	<b>&lt;0.01</b>
	Treatment $\times$ Species	4.05	3	0.257
<i>Motionless</i>	Trial	26.07	1	<b>&lt;0.001</b>
	Treatment	0.18	1	0.668
	Species	93.87	3	<b>&lt;0.001</b>
	Trial $\times$ Treatment	0.16	1	0.691
	Trial $\times$ Species	19.06	3	<b>&lt;0.001</b>
	Treatment $\times$ Species	17.17	3	<b>&lt;0.005</b>
<i>Concealing</i>	Trial	3.06	1	0.080
	Treatment	4.14	1	<b>&lt;0.05</b>
	Species	31.80	3	<b>&lt;0.001</b>
	Trial $\times$ Treatment	0.02	1	0.882
	Trial $\times$ Species	7.01	3	0.071
	Treatment $\times$ Species	26.26	3	<b>&lt;0.001</b>
<i>Grooming</i>	Trial	10.73	1	<b>&lt;0.005</b>
	Treatment	1.29	1	0.256
	Species	51.16	3	<b>&lt;0.001</b>
	Trial $\times$ Treatment	0.23	1	0.633
	Trial $\times$ Species	11.45	3	<b>&lt;0.05</b>
	Treatment $\times$ Species	4.71	3	0.194

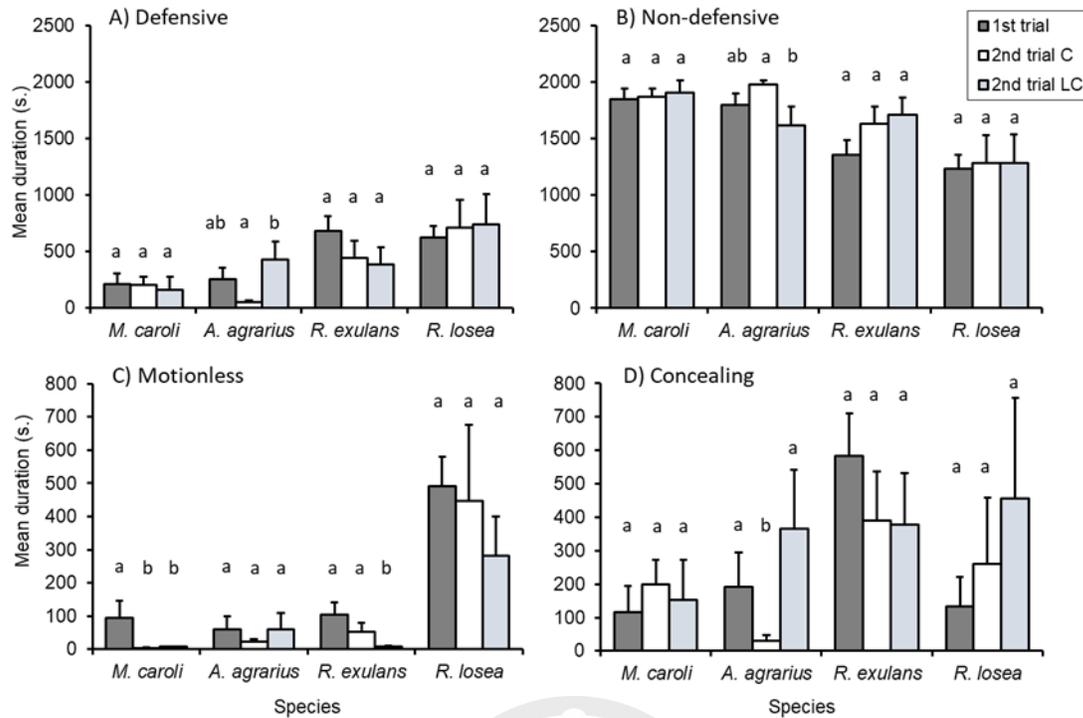
## Figures



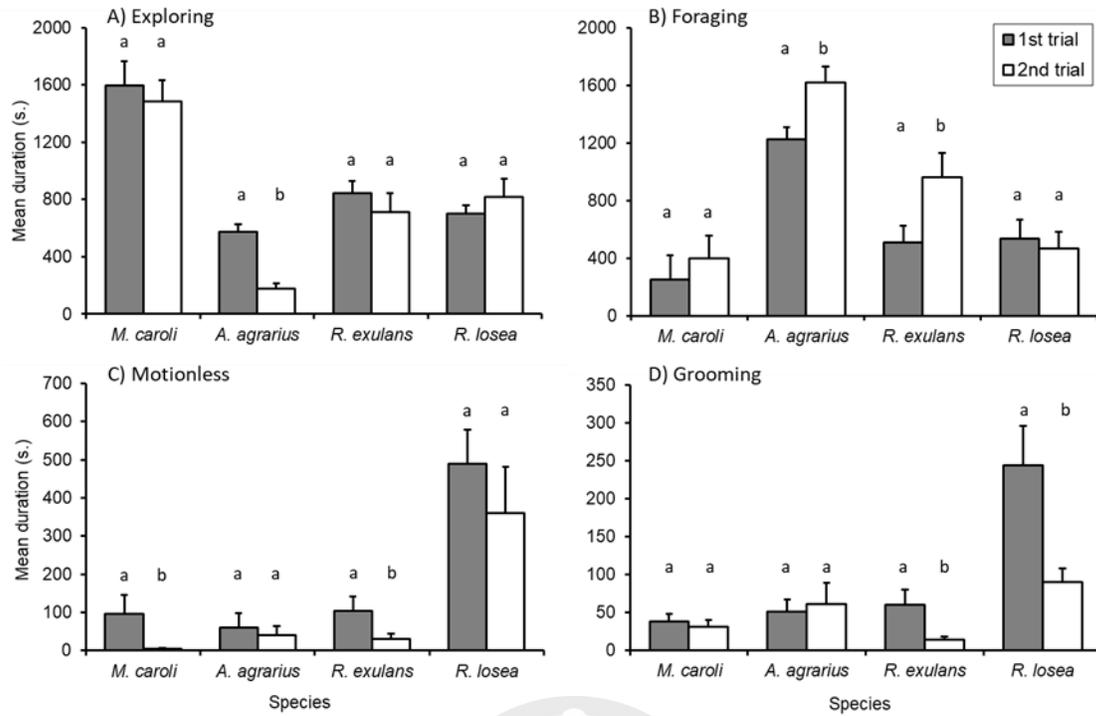
**Figure 2.1.** Schematic of the base of the test arena in the trials. The divisions of the different sections are marked with dashed black lines. The numbers correspond to the specified section. Section 3 included both the area with the food tray and stimulus. Stimulus refers to treatment apparatus.



**Figure 2.2.** Mean duration (out of 2100 seconds) of behavioral responses between species during the first trial; A) Defensive and non-defensive categories, B) All duration-based behaviors. Error bars represent standard error of the mean. Differences in letters above each response variable indicate significant differences based on post hoc analysis between species groups.



**Figure 2.3.** Mean duration (out of 2100 seconds) of A) Defensive and B) Non-defensive behavioral categories, C) Motionless, and D) Concealing. Each response variable is compared between species, treatment group and trial. 1st trial comprises both treatment groups. ‘2nd trial C’ refers to the control group during the second trial. ‘2nd trial LC’ refers to the leopard cat odor group during the second trial. Error bars represent standard error of the mean. Differences in letters above each species indicates significant differences based on post hoc analysis between subgroups: 1st trial, 2nd trial C, 2nd trial LC.



**Figure 2.4.** Mean duration (out of 2100 seconds) of behaviors A) Exploring, B) Foraging, C) Motionless, D) Grooming. Each response variable is compared between species and trial. Error bars represent standard error of the mean. Differences in letters above each species indicates significant differences based on post hoc analysis between 1st trial and 2nd trial for that species.

## **Chapter 3: Of mice and cats: inter-specific variation in prey responses to multiple predator cues**

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**Abstract**

In disturbed landscapes prey face a multitude of risks and must respond accordingly to ensure their survival. Rodents, common prey to many predators, have been equipped with antipredator responses, which includes the ability to discriminate predator odors through olfaction and subsequently modify their behavior. Furthermore, heterogeneity in habitat characteristics, such as vegetation cover, may vary in perceived risk for rodents and act as indirect cues of predation risk. In this comparative study, I investigated the effects of direct (predator odors), and indirect (vegetation cover) cues of predation risk on the foraging behavior of multiple murid rodent prey species in a modified landscape of northwestern Taiwan. With the use of the giving-up density (GUD) framework and camera trap observations, I tested whether rodents altered their foraging behavior depending on microhabitat characteristics and exposure to predator odors of three felids: the native leopard cat (*Prionailurus bengalensis*), the introduced domestic cat (*Felis catus*), and the exotic bobcat (*Lynx rufus*). The consumption of seeds was not affected by predator odors, but rather by microhabitat type; rodents consumed more seeds in food stations under vegetation cover compared to exposed stations. Based on the camera trap observations, the two species responsible for the seed predation in the food patches were *Apodemus agrarius* and *Rattus losea*. The smaller mouse species *A. agrarius* had a much higher propensity to visit and forage from the food stations compared to the larger rat species *R. losea*, irrespective of predator odor type. Additionally, *A. agrarius* exhibited bolder behaviors compared to *R. losea* demonstrated by a higher proportion of time spent foraging in the experimental food patches. The seed consumption results indicate that indirect cues, such as microhabitat, may play a larger role in governing foraging activity compared to predator odors, since exposed areas may reflect high risk from multiple predator taxa. These rodent species may have a proactive approach to their microhabitat use, illustrated by concentrated foraging activity under vegetation cover. Finally, the species-level differences observed in this study indicate that the smaller species confers more boldness compared to the larger species, which reinforces the connection between behavior and pace-of-life, and further elucidates how the behavior of different prey species may not be interchangeable in contexts of risk.

**Keywords:** predation risk, foraging, microhabitat, consumption, predator odor, behavior, boldness, pace-of-life

## Introduction

Ubiquitously, prey navigate their environments while exposed to risks that can have far-reaching effects. The strong selective force of predation can govern morphological, physiological, life history, and behavioral traits of prey (Anson et al., 2013; Hermann & Thaler, 2014; Bedoya-Perez et al., 2019). Predator effects can be consumptive, which involves direct predation or the killing of prey, which influence prey demographics (Preisser & Bolnick, 2008). Non-consumptive effects involve perceived predation risk, which can trigger antipredator behavioral responses in prey (Werner & Peacor, 2003; Moll et al., 2017). Antipredator behaviors can be costly and may result in energetic and/ or physiological consequences, which can, in turn, affect the fitness of prey (Preisser et al., 2005; Creel & Christianson, 2008; Bedoya-Perez et al., 2019). For example, the ‘predator sensitive foraging hypothesis’ postulates that prey will constrain their foraging activity due to increased vigilance, or other defensive behaviors, with subsequent energetic costs (Sinclair & Arcese, 1995; Anson et al., 2013). However, these same antipredator adaptations are what help keep prey alive by reducing encounters with predators.

Many mammalian prey species have highly developed chemosensory systems and use olfaction to discriminate predators (Eisenberg & Kleiman, 1972; Dielenberg & McGregor, 2001). Predator cues, such as odors, have been found to induce antipredator responses in mammal prey (Apfelbach et al., 2005; Parsons & Blumstein, 2010; Apfelbach et al., 2015). These responses may include modulating space use, decreased activity, cessation of foraging, immobility, and hiding (Blanchard & Blanchard, 1989; Apfelbach et al., 2005; Takahashi et al., 2005). For instance, according to the ‘predation risk allocation hypothesis’, during periods of high risk (i.e. the presence of a predator), in generally low-risk

environments, prey should maximize their vigilance and suppress their foraging efforts and activity (Lima & Bednekoff, 1999; Moll et al., 2017). Alternately, if the background predation risk is frequently high, then prey should allocate more time and effort to foraging and minimize defensive behaviors during pulses of low risk (i.e. local predators are temporarily absent) (Sih & McCarthy, 2002; Stryjek et al., 2018). Therefore, the strength of antipredator responses and trade-offs prey exhibit may vary temporally, especially in heterogenous environments. Additionally, if prey are continuously faced with high background risk, bold or risky foraging endeavors may be necessary to meet their energetic demands.

Small mammals, specifically rodents, are predated upon by a wide array of taxa; mammalian, avian, and reptilian predators. To address different sources of danger, rodents may utilize environmental cues for assessing contexts of risk (Lima & Dill, 1990; Wolff & Sherman, 2008). While direct risk cues typically involve stimuli from a predator, such as odors, indirect cues include microhabitat features and illumination (Thorson et al., 1998; Farnworth et al., 2018). For example, rodents may view vegetation cover as safe refuges and factor in the distance from these sheltered areas when making decisions concerning activity (Brown & Morgan, 1995; Searle et al., 2008). Intuitively, in exposed microhabitats prey are often at higher risk to various predators and will attenuate their foraging behavior (Orrock et al., 2004; While & McArthur, 2005). Moreover, there is mounting evidence supporting the relative importance of indirect cues as drivers of predation risk (Pusenius & Ostfeld, 2002; Orrock et al., 2004; Verdolin, 2006; Preisser et al., 2007; Farnworth et al., 2020). Therefore, indirect risk cues, namely uncovered microhabitat, may reflect high predation risk due to exposure to multiple predator taxa including birds of prey,

mammalian carnivores, and reptiles (Orrock et al., 2004; Verdolin, 2006; Hunter & Barrett, 2015).

Prey responses to direct cues, specifically predator odors, may vary depending on the system, community structure, evolutionary history between focal predator and prey, and behavioral variation of prey (Apfelbach et al., 2005; Réale et al., 2007; Parsons et al., 2018). In real-world field conditions with multiple prey species, inter-specific variations in behavioral responses to risk may exist, therefore, comparative approaches should be incorporated to better understand the importance of risk cues on prey communities.

Behavioral variation of prey may arise from differences in pace-of-life (POL). The POL hypothesis posits that closely related species should differ in a collection of physiological, such as metabolic rate, and morphological, such as body size, traits that have coevolved with life histories (Stearns, 1983; Wikelski & Ricklefs, 2001). These variations in life history fit a fast-slow continuum (Wikelski et al., 2003; Dammhahn et al., 2018). In mammals, small species have been documented to exemplify fast paced life histories with a prioritization of current reproduction over survival due to their short life spans, whereas larger species with longer life spans adopt slower life history strategies favoring survival over reproduction (Ricklefs & Wikelski, 2002; Dobson & Oli, 2007). There is growing evidence that behavior is associated with POL (Sih et al., 2004; Réale et al., 2007; Stamps, 2007; Dammhahn et al., 2018). For instance, smaller species with fast life histories are expected to demonstrate behaviors conferring boldness, fast exploration, and exploitation of resources, whereas larger species with slower life histories may be more cautious in response to risk (Ricklefs & Wikelski, 2002; Stamps, 2007; Réale et al., 2010; Sol et al., 2018). Studies have tested both intra- and inter-specific behavioral variation of small

mammals to risk in artificial conditions (Martin & Réale, 2008; Cremona et al., 2015; Best et al., 2020), but examining inter-specific variation of fine-scale behaviors in a natural setting remains relatively unexplored.

Prey responses to predator cues may also depend on the evolutionary history of the predator-prey relationship. Invasive species pose severe risks to their native counterparts due to an absence of heritable experiences in the form of biological interactions, which includes competition and predation (Dickman, 1996; Stokes et al., 2009). For instance, native prey may lack adequate antipredator defenses to introduced predators (Kovacs et al., 2012; Jolly et al., 2018). Without sufficient evolutionary and ecological experiences between a novel predator and native prey, prey may be naïve to predator cues and unable to respond accordingly, adhering to the naïveté hypothesis (Carthey & Banks, 2018; Carthey & Blumstein, 2018). Alternatively, if native prey have eco-evolutionary context with a native predator, then introduced predators of the same ‘archetype’ (i.e. ecologically similar traits) as the native predator may elicit prey antipredator behaviors (Cox & Lima, 2006; Carthey & Blumstein, 2018). Therefore, native prey, such as rodents, may have differential responses to the olfactory cues of a native predator, an introduced predator, and an exotic, unfamiliar predator.

A common approach to testing the impact of predation risk on foraging behavior of wild, free-ranging prey involves giving-up density (GUD) experiments. GUD can be defined as the density of food remaining in a patch after foraging has ceased; where the risk of predation outweighs the benefit of acquiring food (Brown, 1988). These methods are often used to assess the trade-offs between risk and energetic rewards (Brown, 1988; Bytheway et al., 2013; Cremona et al., 2014; Welch et al., 2017). Although GUD experiments can

provide an overall quantitative assessment of perceived predation risk of prey, when operated alone there are limitations toward the finer-scale behaviors of prey in response to risk, such as species-specific responses (Bedoya-Perez et al., 2013), which may have considerable ecological importance and shed light on any risk-related behavioral variation, especially in systems with multiple prey species. Therefore, complementing the GUD framework with video observations via remote sensing camera traps provides a more in-depth analysis of the behavioral traits of the foragers and the processes involved in foraging versus risk trade-offs (Bedoya-Perez et al., 2013; Caravaggi et al., 2017; Smith et al., 2020). For instance, species-specific GUD responses to varying risk contexts (e.g. different predator odors) may be concealed by the net result of the community-level GUD responses, if different prey species have opposing responses. This caveat could be resolved with the addition of camera traps to the GUD design.

Rodents, on a global scale, are pervasive pests that are responsible for devastating losses to the agricultural industry (John, 2014). Conventional practices for rodent management, such as traps and rodenticides, are not without limitations (Meerburg et al., 2014; Bedoya-Perez et al., 2019). For instance, pest rodent populations may exhibit neophobia to rodenticide baits (Inglis et al., 1996; Bedoya-Perez et al., 2019), or develop resistance over a few generations to commonly-applied rodenticides (Buckle, 2013; Meerburg et al., 2014). Additionally, the use of rodenticides may have adverse effects on other wildlife, whether it be through cascading effects or direct contact (Gabriel et al., 2012; Elliott et al., 2014; Lohr & Davis, 2018). Therefore, the effects of predator odors inducing antipredator behavioral responses in captive-reared rodents (Dielenberg & McGregor, 2001; Apfelbach et al., 2005; Takahashi et al., 2005; Hegab et al., 2014) has evoked insights into exploring

innovative pest control management. These pest control practices could involve manipulating predation risk with the use of predator olfactory cues to instigate defensive behaviors in pests (Krijger et al., 2017), such as spatial avoidance and reduced activity. It is already possible to purchase a variety of commercially-available predator odors intended for use as pest deterrents (e.g. PredatorPee® Inc.). The application of the theoretical framework of predation risk towards pest management is not without challenges though, as the efficacy of predator odors encouraging fear-related responses in wild rodents is inconsistent. In fact, several studies conducted in both artificial (Bramley & Waas, 2001; Cremona et al., 2015; Best et al., 2020) and natural (Orrock et al., 2004; Stryjek et al., 2018; Garvey et al., 2017) conditions have found predator odors to have no effect on wild rodent behaviors. The variability in rodent responses to predator odors may be explained by intra- and inter-specific behavioral variation, rodents exploiting the cues to gather information about their environment, as well as physiological state (Parsons et al., 2017; Bedoya-Perez et al., 2019; Best et al., 2020). Thus, the effectiveness of predator odors in suppressing rodent non-defensive behaviors (e.g. exploration, foraging, activity) may be system-dependent, and will require further research at a localized scale in areas where rodents cause damage to agriculture.

In northwestern Taiwan, where there is considerable agricultural activity, one of few viable populations of the predator the leopard cat (*Prionailurus begalensis*) (Kerr 1972) can be found. Over the last century, the distribution and population size of leopard cats has drastically declined in Taiwan, so now they only occupy a few regions of western Taiwan (McCullough, 1974; Pei et al., 2014). Leopard cats are listed as endangered and protected under Taiwan's Wildlife Conservation Act. Concomitant to the population decline of

leopard cats, free-ranging domestic cats (*Felis catus*) have become more widespread and abundant in Taiwan. Moreover, efforts to control the growing free-ranging population of domestic cats through programs such as trap-neuter-release (TNR) have remained largely unsuccessful (K.J.C. Pei, pers. comm., 2019), which is consistent with programs enacted in other countries (Winter, 2004). Not only do the two cat species share similarities in their diets with rodents as a major constituent (Chuang, 2012; Hunter & Barrett, 2015), but in parts of northwestern Taiwan there is overlap in their habitat and distribution (I.N. Best, unpublished data). Therefore, understanding the effects the two felid predators have on rodent prey could provide implications for the ecological importance of their cues.

This comprehensive study combined the capabilities of camera trap monitoring to the GUD framework to assess quantitative responses to risk, as well as fine-scale behaviors representative of two prey species. I investigated how direct (predator odors of three species) and indirect (microhabitat, exposed vs. covered) cues of predation risk influence the spatial and foraging activity of rodent communities in a region with ample agricultural activity. I employed a comparative approach to examine the effects of predator odors from a native predator (leopard cat), an introduced predator (domestic cat), and an unfamiliar, exotic predator (bobcat *Lynx rufus*), on rodent foraging behavior. With the use of experimental food patches and camera trap observations, I assessed how direct and indirect risk cues affected rodent behaviors at both the community and species level. Based on the camera trap data, I also tested for behavioral variation between species. I predicted that (1) of the three predator odors leopard cat cues would have the strongest effect, (2) rodents would forage more from experimental food patches in covered microhabitat, (3) there would be a combined effect of predator odor and microhabitat; rodents would have the

lowest foraging activity at exposed food patches with leopard cat odor, and (4) prey species would differ in their behaviors with the smaller species displaying more boldness.

## Methods

### *Study area*

I conducted the experiments in Zhuolan township, Miaoli County (24.31° N, 120.83° E) of northwestern Taiwan (Figure 3.1). This region is low elevation (< 1000 m) and comprises modified landscape with agricultural fields, namely orchards, and human settlements, as well as secondary forest corridors and shrubland habitat.

Based on preliminary surveys I determined that this area had high leopard cat activity (I.N. Best, unpublished data). Other small carnivores that inhabit the area include ferret badger (*Melogale moschata*), masked palm civet (*Paguma larvata*), and crab-eating mongoose (*Herpestes urva*). There are also the introduced species domestic dog (*Canis lupus familiaris*) and domestic cat (*Felis catus*), which both occur as free-ranging and as pets. The rodent species observed in this area include the lesser ricefield rat (*Rattus losea*), the striped field mouse (*Apodemus agrarius*) and the Ryuku mouse (*Mus caroli*). Both *R. losea* and *A. agrarius* are predated upon by leopard cats (Chuang, 2012). Therefore, due to the presence and activity of both leopard cats and domestic cats, this area provided the opportunity to test for any differential responses of prey to each cat's respective odor.

### *Predator odor*

I used odor cues from the native leopard cat, introduced domestic cat and exotic bobcat. All odor samples were obtained from captive individuals. Leopard cat fecal samples were collected from one individual housed at Pingtung Rescue Center at National Pingtung University of Science and Technology and one individual from Taipei Zoo. Domestic cat

fecal samples were obtained from two pet cats of our colleagues. Donor individuals from both cat species were considered healthy and fed high protein diets. Fresh feces of both types of cats were retrieved, placed in airtight, resealable plastic bags, and stored in a freezer at -20 °C until later use. Samples were stored in a freezer for no longer than one month. At the time of the experiment, the feces were thawed, crushed, pooled together and diluted to a mixture consisting of 30 g feces and 150 mL distilled water for both the leopard cat and domestic cat treatments. These pooled solutions were prepared to avoid any potential bias since the volatile compounds of feces may vary pertaining to individual (Martin et al., 2010; Navarro-Castilla & Barja, 2014). Additionally, similar ratios for fecal solutions have been used in other predation risk studies (Kovacs et al., 2012; Cremona et al., 2014; Cremona et al., 2015). The same homogenous mixture for a predator odor was applied to all the assigned stations during the experiment. For the bobcat odor treatment we used urine samples purchased from PredatorPee® Inc. (Maine Outdoor Solutions, Maine, USA). Bobcats were chosen as the exotic predator because they are of a similar size to leopard cats and domestic cats, and they also predate on rodents (Hunter & Barrett, 2015). Therefore, applying the odor of bobcats made it possible for a comparative approach testing the risk cues of a native, introduced and exotic predator.

***Experiment 1: Indirect vs. direct cues of risk on rodent seed consumption***

This experiment was conducted during the new moon phase from February 20<sup>th</sup> – February 26<sup>th</sup>, 2020. This timeframe was selected to control for varying degrees of luminosity. Illumination is another indirect cue of predation risk and has been found to influence prey behavior (Prugh & Golden, 2014); moonlight can inhibit foraging activity of rodents (Orrock et al., 2004; Farnworth et al., 2019). I performed a GUD experiment to

investigate foraging behavioral responses of rodents in different microhabitat conditions coupled with different predator odors. However, because I replenished the food content daily during the experimental periods, I applied a more broad definition of the GUD framework by focusing on seed consumption, which more accurately reflects harvesting rate (Brown, 1988; Bedoya-Perez et al., 2013). I established three sites in the study area, each at least 500 m distance apart to maintain spatial independence of rodent populations. Each site comprised similar habitat and were inhabited by *R. losea* and *A. agrarius*.

At each site I deployed 16 experimental food patches (hereafter stations) in transects with 8 stations placed under vegetation cover (shrubs, grasses, small trees) and 8 stations exposed (1 m from vegetation) for a total of 48 stations (Figure S3.1). The 16 foraging stations were divided into 8 ‘pairs’ at each site; a pair was comprised of 1 covered station and 1 exposed station set at 3-5 m apart. The transects of ‘pairs’ of stations were at intervals of 30-50 m. An objective of this design was to allow the same rodent individual to access and forage from all containers at a site. In this experiment, microhabitat type was defined as either with vegetative cover (covered) or without (exposed). Incorporating microhabitat type into the design allowed for the testing of different contexts of risk (Orrock et al., 2004), i.e. indirect vs. direct. The vegetative ground cover of the ‘covered’ and ‘exposed’ stations were measured to be 50-90% and less than 10%, respectively. These measurements were taken using a 1 m<sup>2</sup> quadrat at the time of the experiment. During the preliminary experiments with the use of camera trap observation, I determined appropriate food items and apparatus to use for the foraging stations. Each food station consisted of a transparent plastic container (28 X 19 X 14 cm, 5 L) containing 10.0 g of millet seed mixed thoroughly in 800 g of extra-fine sand substrate. All containers were covered by a clear plastic lid to

prevent non-target species entry, which is a common design of GUD experimental apparatus (Bytheway et al., 2013; Cremona et al., 2014; Crego et al., 2018). In every container I drilled a hole (44 mm diameter) at both ends to allow access to the target rodent species. During the experimental period insects were not observed to affect the seeds in the containers. Based on the preliminary trials, to restrict small birds from exploiting the seeds in the containers I affixed rubber tubes (40 mm diameter, 44 mm length) to the holes at each end. This modification did not deter rodents from entering the containers. During the preliminary trials, I was also able to confirm that the species *R. losea* and *A. agrarius* foraged from the experimental food patches. To control for any potential artefacts of the enclosed foraging container on rodent behavior, I conducted another experiment with ‘lidless open’ foraging containers (Please see *Experiment 2: Inter-specific variation in behavioral responses*).

Experiment 1 consisted of two rounds of two consecutive nights of testing. There was a two-night interval of no testing between the two rounds to make sure any lingering odors from the predator cue treatments had sufficiently dissipated. During both rounds on the first night, the predator odors were not applied to the foraging stations. Therefore, the first night provided a baseline of rodent foraging activity and permit before- and after-predator treatment comparisons. On the second day of testing (during both rounds) at least one hour before dusk, predator odor treatments were applied to the foraging stations. I employed a stratified sampling design to ensure that at each site a given foraging station was not assigned the same odor during both rounds. The treatment apparatus consisted of a tag made of highly absorbent cotton material affixed to a wooden stake (25.4 cm long). Depending on the assigned odor type, the tags were soaked in leopard cat fecal mixture,

domestic cat fecal mixture, bobcat urine, or distilled water for the non-odor control. At each station, the treatment apparatus was placed adjacent to the foraging container; in the middle of each end (entrance) of the container.

One week prior to the experiment, food stations were introduced to the sites and rodents could forage freely without any of the predator odor cues. During the experimental period, in the morning after each night of testing, I checked all stations for animal visitation, based on footprints and/ or feces, and foraging activity. The contents in the containers were sieved and the remaining amount of millet seeds were weighed ( $\pm 0.1$  g) using an electronic scale. I then calculated the amount of seeds consumed for each foraging station to determine a *seed consumption* measurement, which was used as a proxy for GUD. The contents of the food containers were replaced, refilling the seeds to 10.0 g.

#### ***Experiment 1: Inter-specific variation in behavioral responses***

At a subset of the foraging stations at each of the three sites, I set up camera traps to provide additional, finer-scale details of the foraging behavior of the rodents. This component of Experiment 1 was performed in tandem with *Experiment 1: Indirect vs. direct cues of risk on rodent seed consumption*. Due to logistical constraints, accessibility and concerns about theft, I only set up cameras at four covered stations at each site (overall 12 stations). I also predicted that there would be more activity at covered stations, which was a requirement for the camera trap component of the study. The number of cameras used at each site was to also facilitate a full representation of odor types (non-odor control, leopard cat odor, domestic cat odor, and bobcat odor). I used a total of 12 KeepGuard KG 780 trail cameras (KEEPWAY Industrial Co., Kowloon, Hong Kong). Each camera was affixed to a tree at a height for an optimal field of view of the foraging station apparatus

(1-1.5 m distance). Cameras were set to take 60-s videos with 1-s interval between potential animal triggers and with the sensors set to high. Cameras were active for the full duration of the day (24-hr) during the testing period since I had previously observed rodent activity during the day in the study area during the preliminary study.

A main objective of the two rounds of testing was to maximize the sample size for the stations equipped with camera traps (4 per site). During each round the stations with camera traps at each of the three sites were assigned different predator odors ( $n = 3$  for each odor type during one round). This design enabled each site to have two replicates of each odor type ( $n = 6$  for each odor type after both rounds). After each night of testing, camera traps were checked for observations and when necessary memory cards and batteries were replaced.

### ***Experiment 2: Inter-specific variation in behavioral responses***

I further investigated the effect of predator odors on the foraging behavior of rodent communities with a secondary experiment involving lidless foraging trays. During preliminary surveys of the study sites, other species of small mammals were observed (I.N. Best, unpublished data), so an objective of this experiment was to test whether these species would visit the food stations. Also, an aim was to test if the larger rodent species, *R. losea*, would be more inclined to visit and forage from the food stations, since it was predicted to be a more cautious species (Best et al., 2020). I performed this experiment from April 19<sup>th</sup> – April 25<sup>th</sup>, 2020, which also took place during a new moon phase. For this experiment, I utilized the same three sites as Experiment 1, and set up five experimental food patches with camera traps at each site (a total of 15 stations). I used the pre-existing locations for the stations that had been equipped with camera traps in Experiment 1 (a total of 12

stations), with an additional camera deployed at another covered station at each respective site. Therefore, for this experiment, I only used stations under vegetation cover since my aims were to focus on identifying the species visiting the food stations and the associated behaviors observed via camera trap monitoring. Additionally, assessing the effect of microhabitat on rodent foraging behavior was not an objective for this experiment. At each site, the stations were set at intervals of 30-60 m. The 'lidless open' stations consisted of transparent containers (25.8 X 16.3 X 6 cm, 1.5 L) without lids and containing 10.0 g of millet seed mixed thoroughly in 800 g of sand (the same contents as Experiment 1). I used the same model of camera with the same settings as Experiment 1.

For this experiment I employed the same temporal design as Experiment 1; consisting of two rounds of two consecutive nights of testing. For both rounds, on the second night of testing I put out the predator odor treatments (non-odor control, leopard cat odor, domestic cat odor, bobcat odor) consisting of the same materials as Experiment 1. The treatment apparatus was placed adjacent to the foraging container. I once again used a stratified sampling design to ensure that each station was not assigned the same odor type twice, and that each site featured all odor groups. The additional camera set up at each site allowed for an additional replicate of a treatment type to further increase the sample size. I made sure during each round that the replicates of the predator odors were different between sites. The sample size (number of stations) for control, leopard cat, domestic cat, and bobcat odor groups was 7, 8, 8, and 7, respectively.

Similar to Experiment 1, in the following morning after each night of testing I checked all stations for animal visitation and foraging activity. Because I could not prevent non-target species from exploiting the seeds in the container due to the lack of lids and seed

consumption was not a main objective of this experiment, I was not concerned with consumption measurements as they may have been invalid. If I observed rodent activity at a station, I replaced the contents recharging the millet seeds to 10.0 g. When necessary memory cards and batteries were replaced in the camera traps.

For this experiment I tried to keep as many parameters of the experimental design the same as Experiment 1. Namely, the primary differences were the type of foraging container (with vs. without a lid) and number of food stations deployed at each site.

### ***Camera trap video data analysis***

The videos from the camera trap data were analyzed manually. From the camera trap video footage of both Experiment 1 and 2, the two rodent species *A. agrarius* and *R. losea* were confirmed to visit the stations and forage. These two species were easily distinguishable due to the size disparity, as well as the distinct stripe along the back of *A. agrarius* individuals. No other species foraged from the stations equipped with cameras. From the camera trap video data, for each species at each station I scored the number of occurrences for the following variables: *triggers*, *visits*, *foraging events*, *interactions*, and *treatment investigation*. *Triggers* were scored when a camera was triggered by an animal's motion and activity. False triggers (no animal visible in the field of view) were not counted. *Visits* were defined as an animal approaching and/ or investigating the foraging station apparatus without entering to forage; the animal was visible in the field of view. *Foraging events* were defined as the animal entering the food container to search for and/ or consume the seeds. Within a single video, an independent measure for a *visit* was considered if an animal left the field of view for a period longer than 15-seconds, and for a *foraging event* if an animal exited the foraging container for longer than 15-seconds. It was also possible

for there to be multiple triggers (i.e. videos) per *visit* or *foraging event*; if either type of event lasted for more than one minute. *Interactions* were observed as intra-specific or inter-specific agonistic encounters between individuals, e.g. chases or fights, as well as group foraging events (i.e. more than one individual foraging from a station at the same time). *Treatment investigation* simply consisted of a rodent approaching, sniffing, biting, or making tactile contact with the treatment apparatus. The scored behaviors were not always mutually exclusive; for example, if an animal visited a foraging station, investigated the treatment apparatus, then entered the food container an occurrence for a *visit*, *treatment investigation* and *foraging event* would be scored.

In addition to the observed response variables, I calculated *foraging per visit*, the proportion of foraging taking place upon visiting a station. *Foraging per visit* could indicate the propensity of a rodent to forage in risky contexts. For this measure, a value closer to 1 would indicate consistent foraging with visits; regularly exploiting the experimental food patch. For each station with rodent activity, I also calculated the proportion of time a rodent foraged when in view of a video and for each species (if applicable). The behavior I focused on was *proportion of time foraging (prop. time foraging)*, since this behavior provided species-level information on variation in boldness (Mella et al., 2015; Patrick et al., 2017; Carthey & Banks, 2018; Montiglio et al., 2018). The other behaviors observed during the video analysis were exploration-related and included locomotive activity outside the food tray, investigation of the food tray and apparatus, and rearing. I decided to not include a time budget for exploring behavior in the analysis to avoid redundancy (i.e. if one behavior increased in proportion, the other

decreased), and to focus on a proxy for boldness. The behavior *prop. time foraging* was scored if the rodent was inside the tray searching for and/ or consuming seeds.

### ***Statistical analysis***

An objective of Experiment 1 was to compare foraging activity via seed consumption at different microhabitat types, therefore if there was activity and seed consumption at only one food station within a pair (exposed and covered), the measurement of the corresponding station was also included in the analysis to represent 2 samples. Another objective was to assess foraging behavior under different contexts: with or without predator odor. If there was foraging activity at a given station on one testing night, but not the other within a round, both measurements were included in the analysis. Including both measurements would help determine the effect of the predator odors (difference between the first trial without treatment and second trial with treatment). If there was no foraging activity for either corresponding stations during either testing night within a round, these station measurements were excluded from the analysis; rodent activity was required to test the hypotheses. Therefore, after combining both rounds the sample size for control, leopard cat, domestic cat, and bobcat odor groups was 20, 20, 22, and 20, respectively. The large and small experimental units considered for this study were *site* and *station ID*, respectively, which were included in the models as random effects. Although moon phase was controlled for, the temporal difference between rounds was considered and incorporated into the analysis. There was no precipitation during any testing night, so this factor did not need to be included in the analysis.

To test for the effects of perceived risk on seed consumption of rodents, I used a linear mixed model (LMM). The fixed effects included in the model were trial (pre-treatment vs.

treatment), odor type (hereafter referred to as *odor*), and microhabitat type. Site, station ID, and round were included in the LMM as random effects. Both two-way and three-way interactions were included in the model for fixed effects as they pertained to my research objectives. More specifically, the interaction between trial and odor would indicate an effect of the predator odor on seed consumption since predator odor treatments were applied on the second night of testing in each round. The raw dataset of consumption values were used for this analysis in order to test for the effect of microhabitat. Although delta values would control for differences in rodent activity between stations, they would also conceal any significant differences between microhabitat type.

For all variables based on the camera trap data, if there was no activity during either trial at a station within a round those measurements were excluded from the analysis. To assess the effect of predator odor on the camera trap response variables I calculated delta values by subtracting the value of the pre-treatment trial from the treatment trial ( $y_2 - y_1$ ) for each station and for each species. This approach helped control for differences in rodent activity between stations and reduced the chances of artefacts appearing in the models (e.g. overall differences between odor groups). Also, for the camera trap variables I did not collect data for both microhabitat types, so I was not concerned with testing for microhabitat differences. The camera trap response variables *visits*, *foraging events*, *foraging per visit*, and *prop. time foraging* were tested with a LMM, which included the fixed effects odor, species, and their interaction. Site and round were incorporated as the random effects.

In order to test my fourth prediction of inter-specific behavioral differences, I also tested the four camera trap response variables: *visits*, *foraging events*, *foraging per visit* and *prop. time foraging*. Since I was only interested in inter-specific comparisons due to the results

of the delta variable analysis (see results of Table 3.2) I used the raw dataset (not delta values) and excluded the factors *trial* and *odor*. A LMM was performed with species as a fixed effect, and round, site, and station ID as random effects. I acknowledge that any inter-specific differences in the count variables, *visits* and *foraging events*, may be attributed to population density variation and not due to behavior. Hence, the analysis of the proportional variables would better reflect inter-specific behavioral variation.

Due to the low and unequal frequency of occurrence for the behavioral variable *interactions*, it was omitted from the mixed model analysis. Because *treatment investigation* could reflect a degree of vigilance, I calculated the proportion of *treatment investigations* per *visits* for each species at each station. For this proportional variable I also used a LMM with odor and species as fixed effects, and round, site, and station ID as random effects. I also tested cross-tabulations with chi-square tests for whether a species was likely to investigate the treatment apparatus upon visiting a station. Cramer's Phi coefficient ( $\phi$ ) was determined for effect size (Breugh, 2003). For all *treatment investigation* analysis only data from the treatment trial was used since the predator odors were only applied during that trial.

For all mixed model analyses I used estimated means with pairwise comparisons incorporating least significant difference for post hoc analysis of main effects and interactions. The camera trap datasets of Experiment 1 and 2 were analyzed separately. Normality of all response variables was determined based on the residuals of the models tested. For all of the statistical analyses significance was considered at  $\alpha = 0.05$ . All statistical analyses were performed with SPSS v.26.0 (IBM, Armonk, USA).

## Results

### *Experiment 1: Indirect vs. direct cues of risk on rodent seed consumption*

Of the 192 foraging opportunities I examined (48 stations X 2 nights X 2 rounds), there was foraging activity in 118 (61.5%). The consumption of seeds by rodents was not affected by predator odor, nor was there an interaction between odor and trial, as well as odor and microhabitat (all  $p > 0.05$ , Table 3.1). Consumption of seeds, and thereby foraging activity, was significantly different between microhabitat type, but there was no interaction between microhabitat and trial. The amount of seeds consumed by rodents was considerably higher at the covered stations compared to the exposed ( $p < 0.001$ ), irrespective of odor and trial (Figure 3.2). On average, rodents consumed 77.4% of the seeds at the covered stations, whereas only 19.0% of seeds were consumed at the exposed stations.

### *Experiment 1: Inter-specific variation in behavioral responses*

I examined 48 foraging observations based on 12 stations (with cameras) for two rounds of two testing nights. *A. agrarius* visited and foraged in 37 (77.1%) of the observations, whereas *R. losea* in only 15 (31.3%). Of the total 1034 triggers, 858 (83.0%) and 176 (17.0%) were attributed to *A. agrarius* and *R. losea*, respectively. Additionally, the average proportion of triggers at a foraging station for *A. agrarius* and *R. losea* were 72.9% and 18.7%, respectively.

Based on the mean delta values (change between the pre-treatment trial and treatment trial), predator odor had no effect on any of the camera trap response variables (all  $p > 0.05$ , Table 3.2). There was also no interaction between odor and species on any of the variables (all  $p > 0.05$ , Table 3.2, Figure 3.3).

I found inter-specific differences for all the response variables in this experiment (all  $p < 0.01$ , Table 3.3). *A. agrarius* had more visits, more foraging events, were more likely to forage upon visiting the food stations, and spent a higher proportion of time foraging compared to *R. losea* (Figure 3.4).

I observed 45 *interactions*, 41 (91.0%) of which were between *A. agrarius* individuals, 3 (7.0%) between *R. losea* individuals, and one inter-specific interaction involving a *R. losea* individual chasing an *A. agrarius*. Among the 41 *A. agrarius* interactions, 32 were chases and/ or fights, and 9 were group foraging events. All *R. losea* interactions were fights and chases.

There was a total of 21 *treatment investigations* with a little over half performed by *A. agrarius* (12, 57.0%) and the rest by *R. losea*. Predator odor had no effect on proportion (number of *treatment investigations* per number of *visits*) of *treatment investigations* ( $F_{3, 19} = 2.23, p = 0.12$ ), nor was there an interaction between predator odor and species ( $F_{3, 19} = 1.93, p = 0.16$ ). There also was no significant difference between species ( $F_{1, 19} = 3.07, p = 0.10$ ), despite the proportion of *R. losea* measured to be more than double that of *A. agrarius* (0.21 compared to 0.09). Alternatively, there was a significant association between visiting a station and investigating the treatment for *R. losea* ( $\chi^2 (1, N = 24) = 9.60, p < 0.01, \phi = 0.63$ ), but not *A. agrarius* ( $\chi^2 (1, N = 24) = 3.79, p > 0.05, \phi = 0.40$ ). When *R. losea* visited the food stations they were more likely to investigate the treatment apparatus.

***Experiment 2: Inter-specific variation in behavioral responses***

In this experiment there were 60 foraging opportunities (15 stations X 2 nights X 2 rounds). The analysis found that there was foraging activity from *A. agrarius* and *R. losea* in 43 (70.0%) and 30 (50.0%) of the opportunities, respectively. Furthermore, 2091 (77.1%) of the total 2713 triggers were caused by *A. agrarius*, with the remainder attributed to *R. losea*. The average proportion of triggers per station was 61.9% for *A. agrarius* and 31.4% for *R. losea*.

Predator odor had a species-specific effect on *foraging per visit* in this second experiment ( $p < 0.05$ , Table 3.2). Post hoc analysis revealed that *foraging per visit* decreased for *R. losea* at stations where domestic cat odor was applied and differed from the delta value of the non-odor control group ( $p < 0.05$ , Figure 3.3). There were no other significant effects or interactions for the variables *visits*, *foraging events*, and *proportion of time foraging* (all  $p > 0.05$ , Table 3.2).

Similar to Experiment 1, all camera trap variables differed between the two species (Table 3.3). *A. agrarius* foraged more often when visiting the open food stations and spent proportionally more time foraging compared to *R. losea* (Figure 3.4).

In this experiment all *interactions* were intra-specific, 185 (97.9%) between *A. agrarius* individuals and only 4 (2.1%) among *R. losea*. Within the *A. agrarius* interactions, 103 were agonistic encounters, such as chases or fights, and 82 were group foraging events, where on some occasions as many as three individuals were observed foraging at the same time. All the *R. losea* interactions were agonistic.

*A. agrarius* and *R. losea* completed 24 (45.0%) and 29 (55.0%) *treatment investigations*, respectively. There was no predator odor effect or species-specific odor effect for the

proportion variable for treatment investigations (Odor group:  $F_{3,30} = 0.48, p = 0.70$ ; Odor group  $\times$  Species:  $F_{3,30} = 1.12, p = 0.36$ ). The proportion of treatment investigations to visits did differ between species ( $F_{1,30} = 16.32, p < 0.001$ ), it was significantly higher for *R. losea* (0.43 compared to 0.08). There was a significant association between visiting a station and investigating the treatment for both *R. losea* ( $\chi^2(1, N = 30) = 26.25, p < 0.001, \phi = 0.94$ ) and *A. agrarius* ( $\chi^2(1, N = 30) = 8.34, p < 0.005, \phi = 0.53$ ). Therefore, in this experiment both species were more likely to investigate the treatment apparatus as oppose to ignoring it when visiting a station.

## Discussion

The findings of this study emphasize the importance of incorporating new technologies into well-established experimental frameworks to better elucidate the intricacies of species behavior in risky contexts. Such was the case by combining camera trap video observations with the GUD method to delve further into understanding species-specific behaviors. The behavioral responses based on both quantitative seed consumption data and camera trap video data are discussed at length below.

The results of this study indicate that rodent foraging efforts toward seed consumption were not affected by any of the predator odors. Overall, seed consumption by rodents did not differ between the predator odors, nor did the addition of the predator odors reduce the amount of seeds consumed. Instead, microhabitat type was a strong predictor of this measurement of rodent foraging activity. Rodents consumed considerably more seeds under vegetation cover compared to being exposed. Although these results do not support two of my predictions (prediction 1 and 3), the significant effect of microhabitat on foraging activity is consistent with other studies. These similarly designed studies targeting

small mammals found that predator odors failed to influence foraging behavior, whereas microhabitat characteristics did (Pusenius & Ostfeld, 2002; Orrock et al., 2004; Orrock & Danielson, 2004; Verdolin, 2006; Spencer et al., 2014). In a study conducted by Pusenius & Ostfeld (2002), the GUDs of meadow voles (*Microtus* sp.) did not change in response to predator odors, but the voles demonstrated a preference for foraging activity under vegetation cover. Comparably, Spencer et al. (2014) found that the native Australian rodent the spinifex hopping mouse (*Notomys alexis*) did not respond to fox (*Vulpes vulpes*) or cat predator odors, but the rodent's foraging behavior was influenced by macro- and microhabitat. Orrock et al. (2004) found that oldfield mice (*Peromyscus polionotus*) altered their foraging efforts in response to microhabitat features (exposed vs. sheltered), but not predator odors. The mice reduced their foraging activity in exposed experimental food patches (Orrock et al., 2004).

I expected rodents to respond to the odors of leopard cats due to their long shared evolutionary and ecological history. With respect to the other predator odors, domestic cat and bobcat, I expected there to be a weaker effect compared to the leopard cat odor, however, the results suggested no difference between any of the odor groups on rodent seed consumption. Although, domestic cat odors may have had species-specific effects on other behaviors. Overall, my results are in accordance with a literature trend, that in natural settings manipulated predator odors have been unsuccessful to elicit antipredator behaviors, such as avoidance or reduced foraging activity, with no difference in effect between odors from native, introduced, or even unfamiliar predators (Orrock et al., 2004; Powell & Banks, 2004; Verdolin, 2006; Shapira et al., 2013; Stryjek et al., 2018). Predator odors have also been ineffective at inducing defensive behaviors in wild-caught rodents in laboratory

conditions (Bramley & Waas, 2001; Cremona et al., 2015; Jolly et al., 2018; Best et al., 2020). For many studies that have observed significant effects of predator odors, the rodents were reared in captivity (Apefelbach et al., 2005; Hegab et al., 2014; Storsberg et al., 2018) and may have been subject to domestication. Domestication of rodents can result in reduced behavioral variation and adaptability, and subsequent elevated responses to foreign odorous stimuli (Price, 1984; Barnett, 2008).

In wild populations of animals the importance of between-individual behavioral variation and individual personality for risk-related situations is becoming more apparent (Sih et al., 2004; Réale et al., 2007; Martin & Réale, 2008; Schuster et al., 2017). It has been found that wild-caught rodents demonstrate variation at the population level in their behavioral responses to risky contexts, such as novel environments or exposure to predator odors, with some individuals bolder than others (Martin & Réale, 2008; Cremona et al., 2015; Jolles et al., 2015; Best et al., 2020; Uchida et al., 2020). For example, in my earlier study conducted in eastern Taiwan wild-caught individuals from four rodent species, including *A. agrarius* and *R. losea*, were exposed to a novel microenvironment and leopard cat odor in a laboratory setting and the behavioral responses were examined (Best et al., 2020). Within species groups, the rodents displayed between-individual variation and individual consistency for foraging behavior – exemplifying a boldness-shyness axis. Additionally, none of the rodents displayed defensive behaviors toward the leopard cat odor, however, in eastern Taiwan leopard cats are absent, so the rodents had no prior encounters with the predator and may be naïve (Best et al., 2020). Within a population, if some individuals are bolder than others then the bolder individuals may be more inclined to exploit resources

even with potential risk, and this behavioral variation may offset the effects of predator odors.

Another possibility for the lack of responses to the predator odors could be due to predator demographics and activity. Leopard cats and domestic cats were both observed in the study area, with high activity for the former. Despite this high level of activity, leopard cats have large home ranges and can travel several kilometers in a day (Ross et al., 2015; Chen et al., 2016). Additionally, in Taiwan it has been found that there is little overlap in home ranges, especially core areas, between leopard cat individuals (Chen et al., 2016). Therefore, rodents may be unable to efficiently assess predator density or likelihood of encounters with predators based on odors alone and may be more dependent on other cues of risk (e.g. microhabitat structure, visual cues) on basing their foraging strategies (Verdolin, 2006; Moll et al., 2017; Gaynor et al., 2019).

In the current study, an explanation for the strong response to the indirect cue of microhabitat variation may be avian predation pressure. For example, in Taiwan, the Black-winged Kite (*Elanus caeruleus*) consumes a high proportion of rodents with its diet comprising up to 90% of *R. losea* and *A. agrarius* (Severinghaus & Hsu, 2015; Hong et al., 2019). This raptor species along with other rodent-consuming birds, the crested goshawk (*Accipiter trivirgatus*) and collared scops owl (*Otus lettia*), occupy low-elevation shrublands and secondary forests, which can be close to agricultural areas (Severinghaus et al., 2012; Hong et al., 2019). These three species have also been observed in the study area (I.N. Best, unpublished data). Therefore, the exposed microhabitat at the study sites may have high background risk that consistently outweighs the rewards of exploiting food resources for rodents. For the same amount of resources available in varying microhabitat

structure, as was the case with the experimental food patches, rodents should prioritize their foraging efforts to maximize their energetic returns in situations where they are not exposed and at high risk from both avian and mammalian predators, which is what was observed in the current study. Under vegetation cover rodents also have quick escape routes (Verdolin, 2006; While & McArthur, 2006; Searle et al., 2008), so if they were to encounter a threat they could quickly flee into dense vegetation.

Camera trap observations confirmed that the species responsible for seed removal were *A. agrarius* and *R. losea*. In both experiments, *A. agrarius* visited more stations compared to *R. losea*. There was also a disparity between the species for the number of visits and foraging events, which can most likely be explained by differences in population density. In Experiment 2, I expected there to be more rodent activity due to the ‘lidless open’ food tray design, especially for the species *R. losea*. The ‘open’ design better reflected a natural food patch with lower foraging costs (Price & Banks, 2017; Cozzoli et al., 2019), but non-target species (e.g. birds) were no longer prevented from accessing the seeds and were observed foraging from some of the stations, which would have made the seed consumption measurements inaccurate. I observed that *R. losea* did visit and forage in a higher proportion of foraging opportunities relative to Experiment 1, but there were still significant differences between the two species. *R. losea* is much larger than *A. agrarius* (up to five times the size), they are more territorial, and can have larger home ranges (Wang & Wang, 2001; Qi, 2008), therefore, they may have a lower population density within a designated area. Furthermore, *A. agrarius* has been found to be more abundant in low-elevation habitat based on capture rates in other parts of Taiwan (Ku & Lin, 1980; Kuo et al., 2011a; I.N. Best, unpublished data). The higher population density of *A. agrarius* may

also be evident from the number of intra-specific interactions observed in both experiments – multiple individuals visited and foraged from a given food station at the same time.

Camera trap results from both Experiment 1 and 2 further suggest that most predator odors had no effect on the foraging behavior of the two rodent species. Because I calculated the delta values for each of the variables included in the models testing the effects of predator odors, differences in rodent activity between stations were controlled for, since predator odors were randomly assigned to stations. For Experiment 1, the delta values for number of visits, number of foraging events, foraging per visit proportion, and proportion of time foraging were not affected by predator odor at the community-level and for each species. For the second experiment, a main objective was to confirm similar community- and species-level responses to the predator odors as Experiment 1, which was the case for all delta variables except *foraging per visit*.

In Experiment 2, there was only a significant interaction between odor group and species for the delta variable *foraging per visit*. This result was most likely attributed to a decrease in *foraging per visit* for *R. losea* with the addition of domestic cat odor during the treatment trial, as was evident from the negative delta value that differed from the delta value for non-odor control group. An explanation for this response could be intra-specific behavioral variation; individuals of the *R. losea* population that visited the stations with domestic cat odor applied more cautious than individuals that visited other stations. As mentioned earlier, individuals of the same species from allopatric populations have exemplified between-individual variation in a series of behaviors in response to manipulated risk (Best et al., 2020). Therefore, it could be expected that this behavioral variation would extend to risk-related experiments in the natural habitat of the focal species (Réale et al., 2007; Patrick et

al., 2017). Some individuals of *R. losea* may be bolder than others and more inclined to exploit available resources, even in the face of risk. Other individuals may show greater neophobia, be more sensitive to predator odors, and less likely to transition from exploration to exploitation. To affirm this possibility and provide further insights toward whether intra-specific behavioral variation mediates predation risk, future studies identifying individuals and examining their behavioral responses to predator odors will be necessary.

The possibility that in Experiment 2 *R. losea* responded to the domestic cat odors for select behaviors should not be dismissed entirely. The close proximity of the study sites to rural settlements and agricultural land may reflect areas with an increased presence of domestic cats. Additionally, since *R. losea* is larger in body size than *A. agrarius*, it is more conspicuous, and may be easier for predators to detect (Preisser & Orrock, 2012; Cozzoli et al., 2019). It is also possible that after an extended period of exposure to an introduced predator species, prey will learn to discriminate the cues (Carthey & Blumstein, 2018). Carthey & Banks (2016) found that the native Australian bush rats (*Rattus fuscipes*) responded to cues of domestic dogs, which are similar in an ecological context to native dingoes (*Canis lupus dingo*), exhibited by increased GUDs. Whether this is the case or not in the current study system necessitates further research and monitoring of domestic cats in the area.

In the present study, a consistent finding for both experiments was the inter-specific difference in *foraging per visit* and *proportion of time foraging*, which can both be considered proxies for boldness. The prioritization of exploitation of resources over exploration in different contexts associated with risk is often linked with boldness (Berger-

Tal et al., 2014; Mella et al., 2015; Patrick et al., 2017). The analysis only included subsets of the full dataset and these variables were proportional, hence differences in population density between the two species should not confound the results. In both experiments, *A. agrarius* was found to have higher proportions of foraging upon visiting the food stations and spending time foraging compared to the larger rat species *R. losea*. These results are in accordance with my previous study (Best et al., 2020), where I found that in laboratory experimental trials manipulating risk, the smaller mice species (including *A. agrarius*) exhibited bolder behaviors, such as more time foraging, compared to the larger rat species (including *R. losea*). Additionally, in that study (Best et al., 2020), *A. agrarius* spent the most time performing foraging-related behaviors compared to the other species. This inter-specific behavioral variation can be linked to differences in POL following a fast-slow continuum (Réale et al., 2007; Wolf et al., 2007; Montiglio et al., 2018; Royaute et al., 2018). Though most empirical studies examining the association between POL and behavior have focused on the individual- or population-level (Cremona et al., 2015; Mella et al., 2015; Dammhahn et al., 2018), the few that have tested for inter-specific variation have been conducted in laboratory conditions (Careau et al., 2009; Best et al., 2020; von Merten et al., 2020). Therefore, the current study provides evidence of inter-specific behavioral differences exemplified by the smaller species, *A. agrarius*, likely demonstrating more boldness compared to the larger species *R. losea*.

An alternative explanation for the differences in the proportional variables, especially *prop. time foraging*, between species could be a disparity in harvesting rate due to, e.g. the larger rat species requiring less time to consume an adequate amount of food as the smaller mouse species. However, when factoring in body weight, metabolism, and energetic

requirements the differences in harvesting rate between the two species *A. agrarius* and *R. losea* were negligible (I.N. Best, unpublished data). Therefore, in order for *R. losea* to consume a sufficient amount of food to meet its energetic needs it would have to spend roughly the same amount of time foraging as *A. agrarius*. Another possibility for the differences between species in the proportional variables could be that the larger species perceived the experimental food patches as low quality and/ or gave up more quickly due to a depleted food availability as a testing night progressed. However, the former seems unlikely since *R. losea* was observed to forage millet seed intently in both another experiment (Best et al., 2020) and during the current study's preliminary trials. Additionally, Experiment 1 was conducted during winter, so it could be expected that food availability in the rodents' habitat would be low. Despite the temporal difference of Experiment 2 and potential higher natural food availability, the proportional variable responses of *R. losea* were consistent with Experiment 1. I also confirmed that the *R. losea* individuals that did forage from the food stations in the current study did not display a reduction in proportion of time foraging as the night progressed and the food supply became more diminished (I.N. Best, unpublished data). For *R. losea* to efficiently assess the quality of an experimental food patch, they would need to enter the foraging trays. However, the results of *foraging per visit* from both experiments suggest that many *R. losea* individuals visited the food stations, but did not enter to forage, which is likely more representative of cautious behavior and neophobia.

In both experiments there were no differences between predator odor groups for treatment investigation performed by either species. However, in Experiment 2 there was a difference between species in the proportion of investigations per visits. *R. losea* had a

higher proportion than *A. agrarius* in both Experiment 1 and 2, despite the former being non-significant. Additionally, it was found that in the first experiment when *R. losea* visited a food station with treatment apparatus, it was more likely to investigate (e.g. sniff) than to ignore the predator odor, whereas there was no association for *A. agrarius*. In Experiment 2, there was an association between visitation of the food stations and treatment investigation for both species, though the effect size ( $\phi$ ) was almost double for *R. losea*. Sniffing odorous substances can reflect exploration and vigilance, which enable prey to process information for risk assessment and learn more about their environment, such as age of the odor signal and type of donor (e.g. competitor, predator) the odor is from (Elliot & Grunberg, 2005; Jones et al., 2016; Carthey & Banks, 2018). It may be that *R. losea*, the more cautious of the two species, more thoroughly investigates a novel, and potentially risky situation before deciding to exploit the available resources. The absence of differences in investigation between different predator odors for the rat may suggest that it is not selective toward a particular odorous stimuli, but will sniff any introduced odor that may be perceived as risky, whether they can discriminate the source or not (Parsons et al., 2017; Bedoya-Perez et al., 2018).

Group foraging was observed in both experiments for the species *A. agrarius*. Group foraging can reflect antipredator behavior, since an individual's net predation risk is reduced (Hamilton, 1971; Bedoya-Perez et al., 2013). Furthermore, an individual may afford to be less vigilant when foraging in a group setting as there are multiple individuals to keep some level of vigilance (Pulliam, 1973; Alexander, 1974). Despite the occurrence of this foraging strategy, I find it unlikely that it was in response to the predator odors. The frequency was quite low at a given station and varied between stations, irrespective of

which testing night. There was an increase in overall frequency in Experiment 2, but that could be due to the ‘open’ design of the food patch. Therefore, the group foraging exhibited by *A. agrarius* may be due to a high population density, sociality and relaxed territoriality (Wolff & Sherman, 2008; Stryjek et al., 2018), as well as a perceived high value of the experimental food patch (Leaver & Daly, 2003; Bakker et al., 2005).

Based on the results of this study, the aptness of applying the mechanisms of predation risk to pest management will need to be revisited and subject to further review for this study system. The push for ecologically-based rodent management to reduce secondary poisoning risks of non-target wildlife has centralized on concepts like the landscape of fear (LOF) (Krijger et al., 2017; Bedoya-Perez et al., 2019), manipulating risky areas for rodent pests with the use predator odors. In my study system, predator odors were largely ineffective at inducing recognizable antipredator behaviors, such as avoidance and reduced foraging, so I would expect the same to be true when applied in farmland, which represents resource-rich modified habitat. Therefore, I suggest testing the efficacy of other risk cues, such as visual or auditory stimuli, which if successful could be integrated into ecologically-based programs for pest control.

## Conclusions

The usefulness of utilizing camera traps in animal behavior and conservation research is garnering more attention (Bedoya-Perez et al., 2013; Caravaggi et al., 2017; Smith et al., 2020), and the findings from this study highlight this with insights for species-specific behaviors toward risk. At the community-level predator odors had no effect on prey seed consumption, whereas microhabitat was a much stronger predictor governing prey foraging preference and activity. Additionally, based on my camera trap data, the smaller species *A.*

*agrarius* was not deterred from visiting or foraging from stations with the addition of any predator odor and demonstrated more behaviors indicative of boldness compared to the larger rat, *R. losea*. These results provide further evidence of the linkage between POL and behavioral traits. Therefore, any applications of manipulated predation risk to pest management will need to factor in inter-specific behavioral variation, as boldness can vary with individuals, populations, and species.



## Tables

**Table 3.1.** Consumption of seeds by rodents affected by trial, group, microhabitat, and their interactions. Group refers to odor groups. Significant values are displayed in bold.

Effect	<i>F</i>	<i>df</i>	<i>P</i>
Trial	0.87	1	0.352
Odor	1.37	3	0.253
Microhabitat	78.87	1	<b>&lt;0.001</b>
Trial × Odor	0.78	3	0.507
Trial × Microhabitat	0.07	1	0.795
Odor × Microhabitat	0.66	3	0.576
Trial × Odor × Microhabitat	1.30	3	0.277

**Notes:** Original seed consumption values from Experiment 1 were used for this analysis,  $n = 162$ .

**Table 3.2.** Mean change (delta) in response variables between trials of rodents from camera trap data of Experiment 1 and 2 for the effects and interactions of group and species. Group refers to odor groups. Significant values are displayed in bold.

Response	Effect	Experiment 1 <sup>*a</sup>			Experiment 2 <sup>*b</sup>			
		<i>F</i>	<i>df</i>	<i>P</i>	Effect	<i>F</i>	<i>df</i>	<i>P</i>
<i>Visits</i>	Odor	0.64	3	0.594	Odor	2.70	3	0.062
	Species	0.01	1	0.907	Species	1.73	1	0.198
	Odor × Species	0.62	3	0.611	Odor × Species	1.57	3	0.216
<i>Foraging events</i>	Odor	0.73	3	0.544	Odor	2.22	3	0.105
	Species	0.01	1	0.925	Species	2.09	1	0.158
	Odor × Species	0.44	3	0.726	Odor × Species	1.09	3	0.368
<i>Foraging per visit</i>	Odor	2.27	3	0.106	Odor	0.70	3	0.559
	Species	1.97	1	0.173	Species	0.15	1	0.700
	Odor × Species	0.85	3	0.478	Odor × Species	3.16	3	<b>&lt;0.05</b>
<i>Prop. time foraging</i>	Odor	1.57	3	0.223	Odor	0.92	3	0.441
	Species	4.17	1	0.052	Species	0.23	1	0.637
	Odor × Species	0.51	3	0.677	Odor × Species	1.66	3	0.196

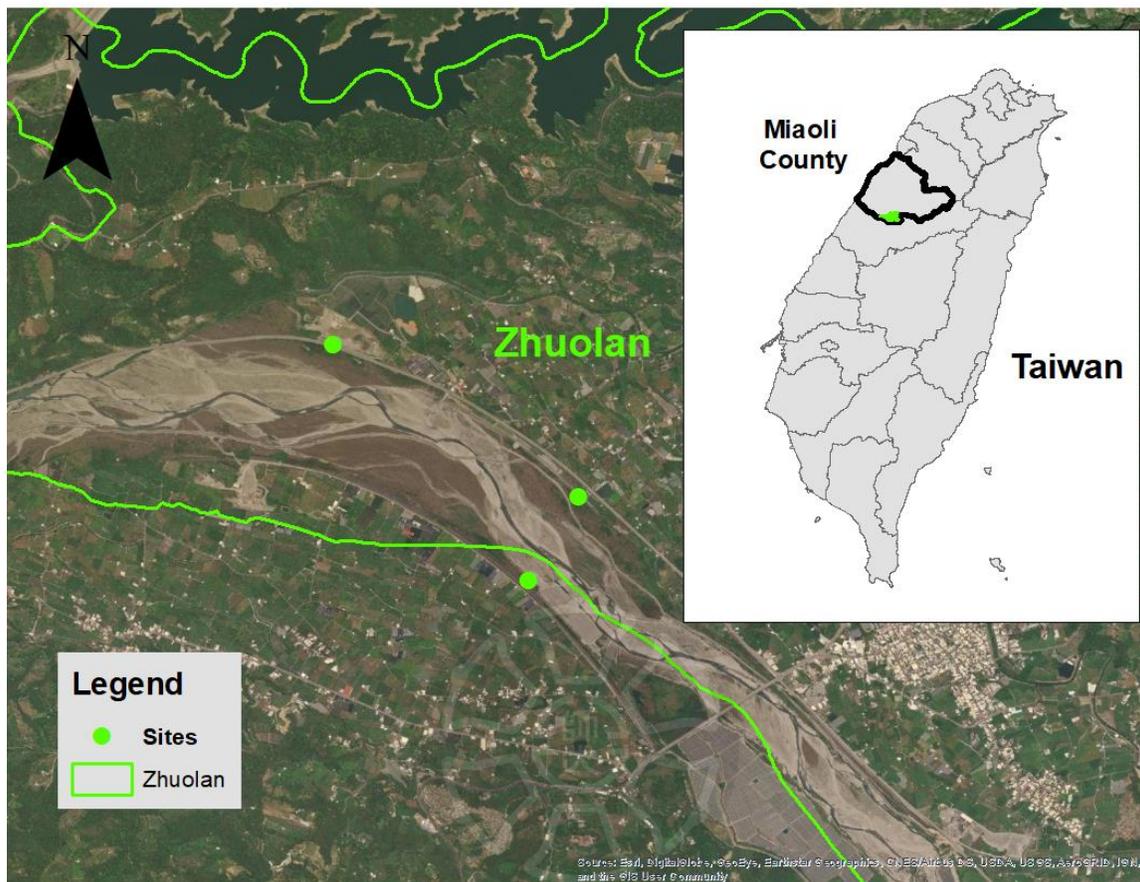
**Notes:** \*Different datasets were used for Experiment 1 (enclosed food containers) and Experiment 2 ('lidless open' food containers); <sup>a</sup> Subset of dataset,  $n = 32$ ; <sup>b</sup> Subset of dataset,  $n = 40$ .

**Table 3.3.** Mean response variables compared between species *A. agrarius* and *R. losea* from camera trap data of Experiment 1 and 2. Significant values are displayed in bold.

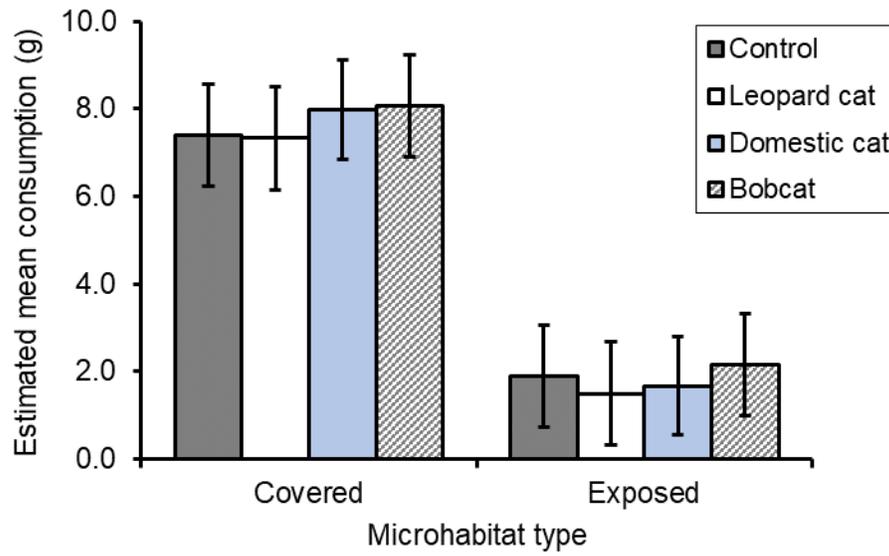
Response	Experiment 1 <sup>*a</sup>			Response	Experiment 2 <sup>*b</sup>		
	<i>F</i>	<i>df</i>	<i>P</i>		<i>F</i>	<i>df</i>	<i>P</i>
<i>Visits</i>	8.04	1	<b>&lt;0.01</b>	<i>Visits</i>	41.11	1	<b>&lt;0.001</b>
<i>Foraging events</i>	9.42	1	<b>&lt;0.005</b>	<i>Foraging events</i>	40.85	1	<b>&lt;0.001</b>
<i>Foraging per visit</i>	11.64	1	<b>&lt;0.005</b>	<i>Foraging per visit</i>	17.51	1	<b>&lt;0.001</b>
<i>Prop. time foraging</i>	8.80	1	<b>&lt;0.005</b>	<i>Prop. time foraging</i>	15.53	1	<b>&lt;0.001</b>

**Notes:** \*Different datasets were used for Experiment 1 (enclosed food containers) and Experiment 2 ('lidless open' food containers); <sup>a</sup> Subset of dataset,  $n = 64$ ; <sup>b</sup> Subset of dataset,  $n = 80$ . Original values were used for this analysis.

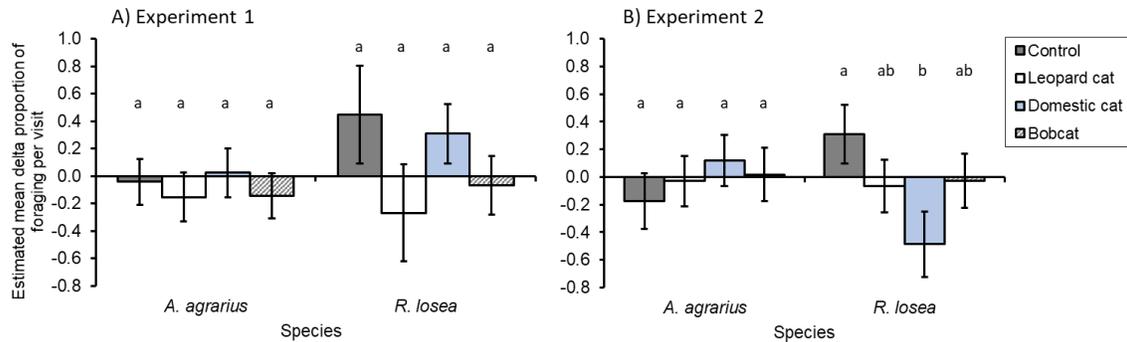
## Figures



**Figure 3.1.** Location of the three sites in the study area of both Experiment 1 and 2 in Zhuolan Township, Miaoli County of northwestern Taiwan.

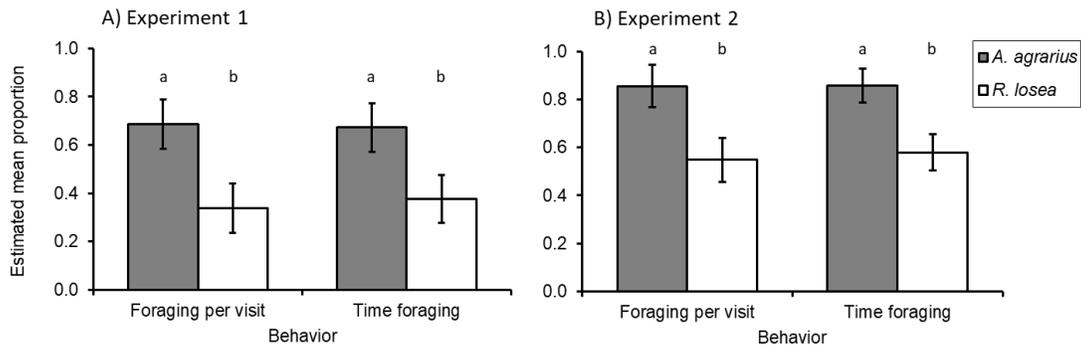


**Figure 3.2.** Estimated mean seed consumption (in grams) by rodents compared between predator odor groups and microhabitat type. Error bars represent the standard error of the mean. Means were taken from only the treatment trial (when predator odors were applied). There were no significant differences between any predator odor groups for either microhabitat type, based on post hoc analysis (all  $p > 0.05$ ). Rodent seed consumption was significantly different between microhabitat type ( $p < 0.001$ ).



**Figure 3.3.** Estimated mean delta on proportion of foraging per visit compared between predator odor groups and species for A) Experiment 1 (enclosed food containers), and B) Experiment 2 ('lidless open' food containers). Error bars represent standard error of the mean. Differences in letters above each odor group indicate significant differences based on post hoc analysis.





**Figure 3.4.** Estimated mean proportion of foraging per visit and time spent foraging compared between the species *A. agrarius* and *R. losea* for A) Experiment 1 (enclosed food containers), and B) Experiment 2 ('lidless open' food containers). Error bars represent the standard error of the mean. Differences in letters between each species indicate significant differences based on LMMs (Table 3.3).



## **Chapter 4: Farmers' knowledge, attitudes and control practices for rodents and other pests in an agricultural region of Taiwan**

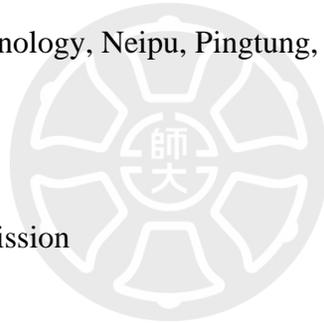
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In preparation for journal submission



***Abstract***

Rodents cause devastating losses on agricultural industries worldwide. The small mammals are common pests for crop varieties such as rice, leafy vegetables, and certain fruits. Common pest management practices include using chemical products, mainly anticoagulant rodenticides. The efficacy of these toxins remains inconclusive, however, and their application can have adverse effects on non-target wildlife from both direct and indirect exposure. In parts of Taiwan, threatened species may be at considerable risk due to their diets comprising a high proportion of rodents. Therefore, in this exploratory study, I surveyed farmers using a structured questionnaire in Miaoli County, northwestern Taiwan, in agricultural areas that overlap with the distribution of the locally endangered leopard cat (*Prionailurus bengalensis*). Based on the completed questionnaires of 126 farmers, rodents were indicated to be the worst pest for the crop rice, but not the crop type vegetables or fruit. Overall, participants perceived fungi to be the worst pest (37.3%), followed by insects (35.7%), and then rodents (19.8%). Only 22.8% of farmers stated they had problems with rodents during both growing and storing of their crops, whereas almost half (45.2%) reported no problems inflicted by rodents. Furthermore, only one-third (33.3%) of farmers indicated they currently use rodenticides, and over three-quarters (77.6%) stated they use other pesticides. The most important predictors for whether farmers use rodenticides were type of crops and extent of problem caused by rodents. Intuitively, farmers were more likely to use rodenticides if they perceived rodents to be very problematic and cause damage. The majority of farmers had negative attitudes towards rodents, which was strongly influenced by experiential factors, and was also a significant predictor for rodenticide use. Participants expressed support to use less chemical-based pest products, but not to stop using them entirely. Therefore, with the information provided by the participants, agricultural profiles of high-risk areas for non-target wildlife can be generated. Additionally, there may be opportunities to implement ecologically based control practices in areas and for crops where rodents are substantial pests.

**Keywords:** rodents, pests, attitudes, knowledge, control, management, rodenticides

## Introduction

Rodents are one of the most widespread taxonomic groups of mammals spread throughout every continent except Antarctica. Their pervasiveness and ability to adapt to highly modified landscape and habitats has had its costs on human health, agricultural industries, and even infrastructure (Meehan, 1984; Wolff & Sherman, 2008; Meerburg et al., 2009a; Han et al., 2015). Rodents can be commensals living in close proximity to humans, which can lead to issues for sanitation, food contamination, property damage and disease risk (Buckle & Smith, 2015; Mendoza et al., 2020). Human health risks can be attributed to rodents harboring ectoparasites and having high reservoir competence for certain zoonoses, such as Lyme disease, scrub typhus and hantavirus (LoGiudice et al., 2003; Kuo et al., 2011a; Khalil et al., 2016; Young et al., 2017). Therefore, it comes as no surprise that rodents are often perceived negatively and viewed as pests. In a more literal sense, rodents' pest-related activities have had devastating impacts on crop yields throughout Asia and on a global scale (John, 2014; Singleton, 2003; Meerburg et al., 2009b; Bedoya-Perez et al., 2019). Crop yield losses usually range from 5-15% in most countries (Singleton & Petch, 2004; Singleton, 2003). However, the losses can be more severe, in the Philippines up to 50% yield losses due to rodents have been reported (Singleton, 2003; Stuart et al., 2011).

To combat these prolific pests, agricultural workers routinely resort to integrated pest management (IPM), which involves the organized use of multiple methods to control pests and reduce their population size (Prakash, 1988; Kogan, 1998; Ehler, 2006). Furthermore, IPM incorporates preventative measures that attempt to be economically efficient and environmentally sensible (Singleton et al., 1999; Ehler, 2006). IPM requires monitoring

from the practitioner and commonly includes physical (e.g. traps) and chemical (e.g. rodenticides) intervention (Ehler, 2006; Singleton et al., 2010). The initial anticoagulant rodenticides (ARs) distributed were first-generation anticoagulant rodenticides (FGARs) and included products such as warfarin (Meerburg et al., 2008; Hong et al., 2019). The subsequent resistance of rodents to FGARs led to the development of second-generation anticoagulant rodenticides (SGARs), which have higher toxicity and potential for adverse environmental effects (Rattner et al., 2014; Elliot et al., 2014).

The consistent and widespread use of both FGARs and SGARs has not only resulted in resistant populations of rodents (Lund, 1984; Lu, 1986; Rost et al., 2009; Meerburg et al., 2014), but also toxicity exposure to non-target wildlife (Rattner et al., 2014; Vyas, 2017; Lohr & Davis, 2018). Non-target wildlife can be affected by direct consumption of poisonous baits or secondary exposure via predation or scavenging of poisoned animals (Rattner et al., 2014; López-Perea & Mateo, 2018; Van den Brink et al., 2018). It is even possible for non-target wildlife to become poisoned through tertiary exposure, such as the consumption of a poisoned mesopredator (Eason et al., 1999; Brakes & Smith, 2005). Chemical-based pesticides (e.g. insecticides, herbicides, fungicides) can also result in acute toxicity of non-target wildlife through multiple routes of exposure, which includes inhalation, dermal contact, and ingestion (Hudson & Haegele, 1984; Berny, 2007). Pesticide residues can consequently proliferate through consumer food chains, especially when exposure to lower trophic levels is consistently high (Franke et al., 1994; Liao et al., 2020). Therefore, for predators that readily consume rodents, such as small carnivores and raptors, ARs and other pesticides can represent a major source of secondary poisoning and threaten their conservation (Sánchez-Barbudo et al., 2012; Hong et al., 2019).

Farmers' pest control practices and subsequent behavior may also be governed by their experiences and attitudes throughout their agricultural careers (Meerburg et al., 2008; Redpath et al., 2015). Experiential factors, which can be based on a single or series of events, can predicate emotion and subjectivity that may supersede rationality for decision-making (Jacobs, 2012; Slagle et al., 2012). For example, a negative experience with wildlife may facilitate strong adverse emotions thereby affecting decisions related to conservation and management (Larson et al., 2016; Castillo-Huitrón et al., 2020). Pertaining to agricultural behaviors, Petway et al. (2019) determined that the most important factors for organic farming decisions were related to life experience and community social norms based on a survey conducted in western Taiwan. It has been posited that in order to design and implement changes to pest management, namely by reducing the usage of chemical products, the behaviors of farmers need to be understood so effective interventions and planning may be conceived (Bondori et al., 2018; Bagheri et al., 2019).

In Taiwan, agriculture constitutes a major component of the economy, accounting for almost 2% of the national GDP (COA, 2020). In 2015, farm crops amounted to 48.8% of all agricultural production, comprised predominantly of the products fruit (37.4%), vegetables (26.3%), and rice (15.3%) (COA, 2020). Similar to other Asian countries (Singleton, 2003), rice is an integral food source in Taiwan and in recent years over 1.5 million metric tons have been produced (COA, 2020). The paramount importance of these plant crops has implications for pest management and the types of products applied. Historically in Taiwan, FGARs have been used since the 1950s to control rodents as pests in agriculture and in urban areas (Hong et al., 2019). Efforts to control rodents increased

in the 1980s with the launch of an anti-rodent campaign by providing SGARs to farmers in the late Autumn annually for free (Lu et al., 2003). Even though the amount of free ARs provided by the government has since declined chiefly due to conservation initiatives, they are still supplied to farmers upon request and can also be acquired by other means (Hong et al., 2018). Hence, it is probable that non-target wildlife face risks of exposure to chemical-based pest products. One such species may be the locally endangered leopard cat (*Prionailurus begalensis*).

Despite being protected under Taiwan's Wildlife Conservation Act, leopard cats still face several threats, and their once extensive distribution of Taiwan is now limited to fragmented regions of the western part of the island (McCullough, 1974; Pei et al., 2014; Chen et al., 2016). The cats are the only indigenous felid of Taiwan and have recently become a conservation priority. They occupy low-elevation habitat and are often observed in modified landscape, including farmland and rural settlements (Chen et al., 2016; I.N. Best, unpublished data). Leopard cats' main prey items are small mammals, notably rats and mice (Chuang, 2012; Hunter & Barrett, 2015). Recently, toxicology reports revealed that deceased leopard cat individuals, victims of road-kill, had traces of SGARs and other pesticides, and had therefore suffered from secondary exposure poisoning (K.J.C. Pei, unpublished data). Furthermore, a recent study conducted by Hong et al. (2019) reported the presence of AR concentrations in liver samples of raptor species in Taiwan. The highest concentrations were detected in the rodent-eating species the black-winged kite (*Elanus caeruleus*) (Hong et al., 2019). The previously mentioned research confirms that top-level predators in Taiwan do face the threat of poisoning via exposure to ARs and other toxins,

and reinforces the need to better understand the locations that may reflect high risk and the pest management behaviors that engender these risks.

Human dimensions and wildlife management studies have been conducted in Taiwan before (St. John et al., 2015; Yen et al., 2015; Best & Pei, 2020; Greenspan et al., 2020), but to my knowledge this is the first focusing on the relationship between pest management of farmers and sources of risk to threatened wildlife. In this exploratory study, I surveyed farmers in an agricultural region in which an endangered species, the leopard cat, is distributed. With the use of a structured questionnaire and adopting the knowledge, attitude, and practices (KAP) approach, I collected information from farmers concerning the types of pests that afflict their crops, their perceived knowledge of rodents as pests, their attitudes toward rodents, and their behaviors for pest control practices. Additionally, I sought to determine the relationships between socio-economic factors, farming-related experience and methods, attitudes towards rodents, and behaviors for pest control (Figure 4.1). I predicted that (1) type of pest and crop type would be associated, (2) farmers that reported more crop damage due to rodents would be more likely to have negative attitudes toward the pests, and (3) extent of damage caused by rodents and attitudes toward the pest would influence pest control behavior. In addition to surveying the extent of rodenticide use, information on the usage of pesticides was collected since pesticides can also be harmful to non-target fauna. This study provided novel information on modified habitat preference of rodents, how they are perceived as pests, factors that may motivate farmers' pest control behavior, and areas where non-target wildlife may be at high risk of toxic exposure. Finally, this research established a basis for determining stakeholder willingness to alter their pest control techniques, transitioning from chemical-based to ecologically-based management.

## Methods

### *Study area*

The study was conducted in the townships Sanyi, Zhuolan, Yuanli, and Tongxiao of Miaoli County, northwestern Taiwan (Figure 4.2). Miaoli County has ample agricultural activity with its economy largely dependent on this food production. The population of Miaoli is 548,863 and roughly 26% are engaged in agricultural activity, which also includes recreational purposes (Miaoli County Government, 2019). Additionally, 33% of the land is designated as farmland for agriculture (Miaoli Land Use, 2020). The county also has initiatives to delineate more land as protected nature reserves for leopard cat conservation and to promote sustainable agricultural practices (Miaoli County Government, 2020), which could result in an increase in rodenticide and pesticide-free farming. The aforementioned townships were selected for the study due to the variation in landscape features and how that may influence crop selection and agricultural practices, as well as the distribution and presence of small carnivores, specifically the leopard cat (Chen et al., 2016; I.N. Best, unpublished data). Additionally, the townships Zhuolan, Sanyi, and Yuanli have been found to have high soil contamination of pesticides based on the hazard index (HI) of chemical residuals (Liao et al., 2020). Therefore, an objective of this study was to assess the extent of rodenticide and pesticide usage by farmers, and to determine any implications for downstream toxicity towards the locally endangered leopard cat and other non-target wildlife.

### ***Data collection***

I utilized a structured questionnaire for this social survey (both English and Chinese versions are available in Appendix C: Supplementary material for Chapter 4). The questionnaire was first drafted in English and then translated to Mandarin Chinese. Preliminary tests of the questionnaire were conducted on eight farmers to help identify any issues or lacking content. Based on the feedback, the questionnaire was revised and included statements and questions to collect data pertaining to socio-demographic variables of participants, information about their farms and farming practices, types of pests and extent of pest-related damages, attitudes toward rodents, and pest control practices and behavior. I decided to not include any questions requesting information on the usage of specific rodenticides or pesticides, such as chemical name or brand name, due to sensitivity issues, since some rodenticides have been banned, and to encourage honesty in responses. Overly sensitive topics may motivate participants to misreport or avoid the content all together (Tourangeau & Yan, 2007; Nuno & St. John, 2015). Rodenticides and pesticides were distinguished from one another in the questionnaire, and pesticides were defined as insecticides, fungicides and herbicides. The questionnaire was designed to take a participant roughly 15-minutes to finish.

Most of the questionnaires were distributed with the help of the local farmer's association centers in each township of the study area. The farmer's association is an extension of the national-level Council of Agriculture, Executive Yuan, and can provide services for farmers locally. These services include banking, technical advice, sale of agricultural products (e.g. pesticides, fertilizer), and sale of farming equipment and tools. Enlisting the aid of the localized association centers enabled access to the target demographic group (i.e.

farmers) to distribute the questionnaire and maximize the sampling effort. Additionally, this method facilitated sampling a wide representation of farmers in the designated townships, since many farmers will visit these centers. All questionnaires were accompanied with a cover letter stating the scope of the survey, affiliated research institutes, anonymity of participant identity, and voluntary consent to participate in the study. Completed questionnaires were returned to staff members at the farmer association centers and later retrieved by myself. I also collected responses of the questionnaire by employing quasi-random sampling. In the agricultural areas of the townships of the study area, a translator and I would ask a random selection of farmers if they would be willing to complete the questionnaire. However, locating farmers at random proved to be challenging, so most of the returned questionnaires were from the association centers. All participants were 18 years of age or older and gave their consent for their responses to be used for academic research. The survey was conducted from June to October 2020.

### ***Data analysis***

The responses of each returned questionnaire, which were in Mandarin Chinese, were translated into English. After going through all returned questionnaires and data cleaning, questionnaire responses from 126 farmers were retained. The questionnaire was divided into four sections for data to be extracted from: background information of farmers (socio-demographic factors) and their agricultural practices, the types of pests that are problematic and the perceived extent of damage, attitudes towards rodents, and pest control practices and behavior.

Based on the information provided by the farmers concerning the main crop they grow, I was able to group their responses into three main crop types: rice, vegetables, and fruits.

Because of the small sample size of completed questionnaires from the township Tongxiao, as well as the close proximity and similar crop types to Yuanli township, I included the responses as part of the Yuanli township group. Main occupation and main income of farmers were found to have high internal consistency ( $\alpha = 0.895$ ) based on Cronbach's alpha (Cronbach, 1951), so only 'main income' was used in the analysis. Types of pests that are problematic for farmers were compared together to establish which pest farmers perceived as the worst. I was also able to determine how problematic farmers viewed each type of pest throughout their crop production process, ranging from no problem to a dual problem. Furthermore, because few farmers reported only post-harvest damage from pests (< 6.5%), pre-harvest and post-harvest problems were combined. Singular problems were defined as a pest causing damage to crops during either the growing (pre-harvest) or storing (post-harvest) stage, but not both. Dual problems involved participants reporting pests causing damage to their crops during both the growing and storing stages. Cross tabulations were performed with chi-square tests to test for associations between the pest-related variables (e.g. *extent of problem*; see Table 4.1) and farming-related predictor variables, which included township, crop type, and crop storage. Due to the low frequency of 'plants' and 'other pests' being reported as problematic pests and since plants were not ranked as a worst pest, this analysis of these pest types was not carried out. For a complete list of predictor variables used in the analysis, please refer to Table 4.1.

Likert scale scores were used for the statements associated with attitudes toward rodents, ranging from 1 (strongly agree) to 5 (strongly disagree). A sixth option (uncertain) was available on the questionnaire; however, these responses were omitted from the analysis. The direction of the Likert scores was due to the wording of the statements; indicating

agreement would suggest negative attitudes towards rodents. Therefore, a lower Likert score represented negative attitudes. In order to evaluate the distribution of agreement (in percentage of participants), the Likert scores were condensed into three categories: agree (1-2), neutral (3), and disagree (4-5). To measure participant internal consistency for these statements, an estimate of Cronbach's alpha was determined ( $\alpha = 0.735$ ). A principal component analysis (PCA) was performed to reduce the number of variables (statements with full Likert scale). I incorporated a varimax rotation in the PCA and only retained the components that explained most of the variance with eigenvalues greater than 1 (following the Kaiser-Guttman criterion: Kaiser, 1991). One component was generated from the PCA and explained 66.0% of the variance, therefore a rotation was not possible. The component reflected farmers' attitudes toward rodents (*rodent attitude* hereafter), with lower values indicating negative attitudes and higher values positive. A main objective in this exploratory study was to determine important explanatory variables for farmers' attitudes toward rodents. Additionally, because there was missing data for many of the predictor variables, in order to avoid an accumulation of missing data and subsequently alter any effect on *rodent attitude*, separate models were performed between each predictor variable and the dependent variable. A generalized linear model (GLM) with a linear function was used to determine the effect of each predictor variable on the component variable *rodent attitude*.

To determine what factors contributed to whether farmers used rodenticides or pesticides (hereafter referred to as *rodenticide use* and *pesticide use*, respectfully) cross tabulations and chi-square tests were performed. Each of these dependent variables was dichotomous with "yes" or "no" as the possible responses. I decided to not use logistic regression

analysis to once again avoid an overaccumulation of missing data and invalidate the models. Additionally, quasi-complete separation may have existed for some predictor variables and the response variables (Albert & Anderson, 1984); e.g. *extent of rodent problem* and *rodenticide use*.

I was also able to assess other pest control behaviors of the farmers, namely willingness to use less and/ or stop using rodenticides and pesticides, based on Likert scores for statements from the questionnaire. Separate statements were included for willingness to use less and willingness to stop using pest control products (i.e. rodenticides and pesticides). The variables for these statements (hereafter referred to as *use less* and *stop using*) were analyzed individually due to the different implications for farmers; some participants may be willing to use less but not willing to stop using altogether. Only responses from farmers who stated they currently use rodenticides and/ or pesticides were included in the analysis. The Likert scale for these statements ranged from 1 (strongly disagree) to 5 (strongly agree). If farmers selected “uncertain” these responses were excluded from the analysis. Relationships between these dependent variables were determined using Spearman rank correlation. Because of the smaller sample size due to only focusing on subsets of the data, ordinal logistic regression including multiple initial independent variables in a model was not performed for the variables *use less* and *stop using*. Instead, to determine appropriate explanatory variables for participant willingness to change pest control behaviors, cross tabulations and chi-square tests were conducted. For the chi-square tests, to reduce the number of subgroups of each dependent variable (e.g. *stop using rodenticides*), the Likert scale was condensed into three categories: disagree (1-2), neutral (3), and agree (4-5).

To address whether farmers' attitudes toward rodents influenced pest control behaviors, GLMs were used with a binary logistic function for the variables *rodenticide use*, *use of traps*, and *pesticide use*. The reference category for the models was set to the lowest value, which was "no" for using the control products. The same model parameters were used to test if estimated annual crop loss affected use of rodenticides or pesticides.

A GLM with an ordinal logistic function was used for the variables *use less rodenticides* and *stop using rodenticides*. The condensed versions of *use less rodenticides* and *stop using rodenticides* were used for this analysis in order to save degrees of freedom. In each model, *rodent attitude* (a continuous variable) was set as a co-variate.

For all cross tabulations, when necessary Fisher's exact tests were used for quality control of the data (Upton, 1992). For each statistical analysis performed significance was considered at  $\alpha = 0.05$ . All statistical analyses were completed with SPSS v.26.0 (IBM, Armonk, USA).

## Results

### *Farmer background information*

For a list of the socio-demographic factors and background information of the farming practices of the participants, please refer to Table 4.2. Based on the responses, most of the participants were male (67.3%,  $n = 107$ ), with around a third (32.7%) female. Roughly three-quarters of the participants' ( $n = 126$ ) main occupation and main income were stated as farming (Table 4.2). The most abundant crop type of the participants was fruit (53.2%,  $n = 126$ ), followed by rice (27.8%) and then vegetables (19.0%).

### *Types of pests and extent of problem*

Fungi was most commonly ranked as the worst pest for participant farming practices (37.3%), followed by insects (35.7%), rodents (19.8%), and other types of pests (3.2%). No farmers selected plants as the worst pest, and 4.0% claimed pests were not a problem. Worst pest was significantly associated with crop type ( $\chi^2(8, N = 126) = 36.78, p < 0.001$ ). The worst pest for rice ( $n = 35$ ) was tied between rodents and insects (both 37.1%). The worst pest for vegetables ( $n = 24$ ) was insects (45.8%) followed by rodents (37.5%). Finally, participants reported that their fruit crops were most afflicted by fungi (58.2%), and then insects (31.3%). Therefore, rodents were more likely to be pests for rice and vegetables, fungi for fruits, and insects were perceived to be problematic for all three crop types. Township was also significantly associated with worst pest ( $\chi^2(8, N = 126) = 32.52, p < 0.001$ ). According to the farmers in the survey, rodents were ranked the worst pests in Sanyi (40.0% of all pests), fungi in Zhuolan (61.1%), and insects in Yuanli (42.9%). Storage of crops was not associated with worst pest ( $\chi^2(4, N = 126) = 2.88, p = 0.594$ ).

About half of the farmers (49.2%,  $n = 126$ ) indicated rodents caused damage to their crops during the pre-harvest, or growing, stage. Only 28.6% of participants stated that rodents caused damage during the post-harvest, or storage, stage for their crops. Moreover, 77.8% of the reported post-harvest problems were from farmers who also had pre-harvest rodent problems. The extent of perceived rodent problems was significantly associated with township, crop type, and crop storage (Table 4.3). In Sanyi the highest proportion of rodent problems were dual (40.0%,  $n = 30$ ), whereas in Zhuolan ( $n = 54$ ) and Yuanli ( $n = 42$ ) the highest proportion of participants reported no problems due to rodents at 55.6% and 45.2%, respectively. For dual rodent problems ( $n = 28$ ) the highest proportion reported

by farmers were in Sanyi and Yuanli, both at 42.9%. Singular rodent problems ( $n = 41$ ) were most common in Zhuolan (48.1%). For crop type, the highest proportion of dual problems by rodents were for rice (42.9%,  $n = 28$ ), and singular problems caused by rodents were for fruit (54.8%,  $n = 42$ ). Farmers who did not store their crops were more likely to have no crop damage from rodents (62.1%,  $n = 29$ ). Insect problems were not significantly associated with township, crop type, or crop storage (Table 4.3). Fungi-related problems were associated with township, crop type, and crop storage (Table 4.3). The highest proportion of both dual ( $n = 22$ ) and singular problems for fungi ( $n = 60$ ) were in Zhuolan (68.2% and 41.7%, respectively) and for the crop group fruit (77.3% and 58.3%, respectively). Almost half of the farmers who store their crops had singular fungi problems (41.2%,  $n = 97$ ).

The average estimated annual crop loss due to pests reported by farmers was  $15.7\% \pm 1.3$  (range = 0 – 50%,  $n = 93$ ). Among the farmers that ranked rodents as the worst pests, the mean estimated annual crop loss was  $14.1\% \pm 2.7$  (range = 2 – 50%,  $n = 19$ ). According to the farmers the average number of different pests during their crop production was  $2.3 \pm 0.1$  ( $n = 126$ ).

### ***Attitudes toward rodents***

Overall, participant attitudes towards rodents were negative based on the three statements included in the questionnaire (Table 4.4). The average Likert score (out of 5) for the three statements was 2.5. The component from the PCA *rodent attitude* was highly associated with all three statements (Table 4.4). Estimated annual crop loss due to pests and *rodent attitude* were not significantly correlated (Pearson's  $r = 0.02$ ,  $p = 0.90$ ,  $n = 70$ ).

Township, age, crop type, and extent of rodent problem all had significant effects on *rodent attitude* (Table 4.5). Farmers from the township Sanyi had the most negative attitudes, whereas those that reside in Zhuolan had the most positive (Figure 4.3A). Farmers who grow vegetables also had the lowest *rodent attitude* scores (Figure 4.3B), therefore the most negative attitudes. Intuitively, farmers with perceived dual problems from rodents also had the most negative attitudes (Figure 4.3D). Farmers below the age of 56 were found to have neutral or positive attitudes, whereas those 56 or older had negative attitudes toward rodents (Figure 4.3B).

### ***Pest control practices and behavior***

Two-thirds of the farmers in the survey stated they currently do not use rodenticides (66.7%,  $n = 126$ ). Of the answers provided for reasons to not use rodenticides, the most common was that farmers think they are ineffective (31.7%,  $n = 63$ ). Other reasons included rodenticides not being necessary, environmentally-friendly farming practices, and the belief that biological factors (e.g. predators) would control rodent populations. Around one third of the farmers stated they use rodent traps, including both lethal and live traps (35.0%,  $n = 117$ ). Only 15.4% of farmers reported using both traps and rodenticides to control for rodents. Contrarily, just over three-quarters of the participants indicated they use pesticides (77.6%,  $n = 125$ ). The most common reason provided for not using pesticides was environmentally-friendly farming practices (42.9%,  $n = 28$ ). 31.2% of the farmers responded that they use both rodenticides and pesticides ( $n = 125$ ). Of the farmers who stated they do not currently use rodenticides, 38.8% disclosed that they have used them before. Only 25.0% of the participants who reported not currently using pesticides indicated they used them before.

When queried about how rodenticides are obtained, the most common response from the farmers was requesting them from the government to be supplied for free (59.3%,  $n = 54$ ). The most common consideration for which rodenticides to use was availability (26.3%,  $n = 76$ ). Other common considerations were effectiveness (19.7%) and environmental friendliness (13.2%). On average, farmers spent \$2111 NTD (\$75 US) per year on rodenticides. For obtaining pesticides, most farmers responded that they purchased them from local stores in their communities (79.4%,  $n = 102$ ). Frequently selected considerations ( $n = 168$ ) for which pesticides to use included effectiveness (21.4%), availability (17.3%), and brands that have been used traditionally (14.3%). Farmers spent an average of \$40,162 NTD (\$1,421 US) annually on pesticides.

Township, crop type, worst pest and extent of rodent problem were found to be significant explanatory variables for *rodenticide use* (Table 4.6). Farmers that live in Sanyi, grow vegetables, ranked rodents as their worst pest, and reported a dual problem from rodents were more likely to use rodenticides (Figure 4.4). Estimated annual crop loss had no effect on *rodenticide use* ( $B = -0.01$ , Wald  $\chi^2 = 0.16$ ,  $p = 0.69$ ,  $EXP(B) = 0.99$ ).

Township, education, number of years farming, worst pest, and extent of fungi problem were significantly associated with *pesticide use* (Table 4.7). A higher proportion of farmers that confirmed they use pesticides are from the township Zhuolan, have less formal education, have been farming for longer, rated fungi as the worst pest for their crops, and have a dual fungal problem for their crop production (Figure 4.5). Estimated annual crop loss was not a significant predictor for *pesticide use* ( $B = 0.00$ , Wald  $\chi^2 = 0.00$ ,  $p = 0.98$ ,  $EXP(B) = 1.00$ ).

Attitudes toward rodents (*rodent attitude*) was found to be a significant predictor for use of rodenticides. Farmers with negative attitudes were more likely to use rodenticides in their farming practices ( $B = -0.74$ , Wald  $\chi^2 = 8.23$ ,  $p < 0.005$ ,  $EXP(B) = 0.48$ ). However, farmers' attitudes did not contribute to whether they use traps ( $B = -0.22$ , Wald  $\chi^2 = 0.96$ ,  $p = 0.33$ ,  $EXP(B) = 0.80$ ) or pesticides ( $B = -0.33$ , Wald  $\chi^2 = 1.62$ ,  $p = 0.20$ ,  $EXP(B) = 0.72$ ).

### ***Willingness to change pest control practices and behavior***

Among the farmers that stated they currently use rodenticides, almost half indicated agreement for willingness to use less (45.9%,  $n = 37$ ), though, far less participants were willing to stop using rodenticides altogether (24.3%,  $n = 37$ ; Table S4.1). Additionally, over half of the farmers stated they think rodenticides are effective (54.7%,  $n = 37$ ; Table S4.1). The average Likert scores (1-5) for *use less rodenticides* and *stop using rodenticides* were 3.24 and 2.70, respectively. *Use less rodenticides* and *stop using rodenticides* were also significantly correlated ( $p < 0.001$ ; Table S4.2).

The only significant independent variable for *use less rodenticides* was worst pest (Table 4.6); farmers who ranked insects as the worst pests had the highest proportion of being willing to use less rodenticides (Table 4.8). Township, main income, and crop type were found to have significant associations with *stop using rodenticides* (Table 4.6). Farmers from the township Sanyi were more likely to be willing to stop using rodenticides (Table 4.8). Additionally, participants whose main income is not from farming and who grow vegetables had a higher proportion of willingness to stop using rodenticides (Table 4.8). *Rodent attitude* was not a significant predictor for *use less rodenticides* ( $B = -0.00$ , Wald  $\chi^2 = 0.00$ ,  $df = 1$ ,  $P = 0.99$ ,  $EXP(B) = 0.99$ ) or *stop using rodenticides* ( $B = -0.20$ , Wald  $\chi^2$

= 0.386,  $df = 1$ ,  $P = 0.53$ ,  $EXP(B) = 0.82$ ). When queried about incentives for willingness to change rodenticide use practices, the most common response was to help protect the environment (29.0%,  $n = 62$ ), followed by protecting other's health (19.4%), protecting personal health (16.1%), and financial compensation (16.1%). Nine farmers stated they were not willing to change their rodenticide use practices ( $n = 36$ ).

Almost two-thirds of the farmers who informed they use pesticides were willing to use less pesticides (65.6%,  $n = 93$ ; Table S4.1). Similar to willingness to stop using rodenticides, only a small proportion of the participants indicated agreement to stop using pesticides (19.4%,  $n = 93$ ; Table S4.1). Furthermore, 71.4% of the farmers currently using pesticides thought they were effective (Table S4.1). The mean Likert scores for *use less pesticides* and *stop using pesticides* were 3.58 and 2.62, respectively. The two variables were also positively correlated ( $p < 0.005$ ; Table S4.2). Additionally, *stop using rodenticides* and *stop using pesticides* were positively correlated ( $p < 0.001$ ; Table S4.2), with high internal consistency for participants' responses (Cronbach's  $\alpha = 0.72$ ). Gender and extent of rodent problem were significantly associated with *use less pesticides* (Table 4.7). The highest proportion of agreement to use less pesticides was from male farmers and those that reported no problems from rodents (Table 4.8). *Stop using pesticides* was associated with township, gender, and crop type (Table 4.7). Farmers from the township Sanyi were more likely to agree to stop using pesticides (Table 4.8). Female participants and those that grow vegetables were less opposed to stop using pesticides (Table 4.8). The most frequently selected incentives for participants changing their pesticide use practices were protecting other's health (26.6%,  $n = 169$ ), protecting personal health (23.7%),

helping to protect the environment (23.1%), and financial compensation (11.2%). Seventeen farmers claimed to not be willing to change their pesticide use behavior ( $n = 88$ ).

## Discussion

In this exploratory study, farmers indicated that they perceive rodents to be problematic and a pest. Although the highest proportion of participants stated that fungi were the most damaging pests, this result is likely attributed to the strong associations between township, crop type, and worst pest; there was a larger sample size of fruit farmers compared to rice and vegetable farmers. About one-fifth of participants claimed rodents were the worst pest overall and rodents were ranked as the worst pest, alongside insects, for the crop type rice. Therefore, it is clear that rodents were a problem for farmers and were responsible for crop losses in the present survey. This finding is consistent with other studies that surveyed farmers in parts of southeast Asia, where rodents were reported to be important pests for rice production (Schiller et al., 1999; Tuan et al., 2003; Brown & Kamphouleo, 2007; Brown et al., 2008; Stuart et al., 2011).

Almost one-half of the farmers in this survey considered rodents to cause damage to their crops during the pre-harvest stage, and slightly more than one-quarter indicated perceived crop damage from rodents during the post-harvest stage. Therefore, the extent of rodent problems for farmers were predominantly singular; rodents causing damage to crops during either the pre-harvest or post-harvest stage. In the case of this study, more farmers perceived rodents to cause damage during the growing stage. A review by John (2014) found that pre-harvest losses due to rodents can comprise a significant proportion of the overall yield losses. Additionally, the farmers in this survey (that ranked rodents as the

worst pest) estimated their annual crop loss due to rodents to be 14.1%, which constitutes overall annual crop loss, and is similar to other estimations of rodent-induced crop loss in Southeast Asian countries; a general range of 5 – 15 % (Singleton, 2003; Brown et al., 2008; Stuart et al., 2011; John, 2014). The higher estimations of annual crop yield losses are typically associated with crops such as rice and maize (Singleton, 2003; John, 2014; Tomass et al., 2020), and can be influenced by environmental and ecological factors, including rodent outbreaks (Meerburg et al., 2009b; Singleton et al., 2010). In the current study, the sample size of the estimation (14.1%) is quite low and since a large proportion of the participants primarily grow fruit and did not perceive rodents to be the worst pest, the annual crop yield losses due to rodents in reality could be invariably higher for farmers with crops that tend to be more afflicted, such as rice or leafy vegetables. In other words, the information provided by the sample of farmers in this survey may not wholly reflect the severity of crop losses due to rodents in Taiwan. Despite this, it is evident that rodents are problematic for farmers in the Miaoli agricultural area, and this survey has brought to attention agricultural systems and locales that are most at risk – rice paddies in the townships Sanyi and Yuanli.

Despite the pest-related problems caused by rodents being largely crop-dependent, participants overall had slightly negative attitudes towards them based on the cumulative mean of the Likert scores for the attitude statements (Table 4.4). For instance, almost two-thirds of the farmers agreed that rodents are a risk to people. This negative perception most likely arises from the potential of rodents transmitting zoonotic diseases (Chin et al., 2000; Meerburg et al., 2009a; Han et al., 2015). If animals have the ability to cause harm they

may be stigmatized and perceived negatively (Batt, 2009; Prokop & Randler, 2018; Castillo-Huitrón et al., 2020).

The socio-demographic variable age had a significant effect on the variable *rodent attitude*. Overall, the older age groups, 56-65 and 65+, had the most negative attitudes toward rodents, which is a consistent finding in relationships between socio-demographic factors and perceptions of wildlife (Suryawanshi et al., 2014; Best & Pei, 2020; Castillo-Huitrón et al., 2020; Greenspan et al., 2020), especially when the wildlife in question are problematic (Røskaft et al., 2007; Morzillo et al., 2011). Older farmers may be more prejudiced toward rodents due to an increased likelihood of experiencing rodent population irruptions accompanied with devastating crop losses during their farming career (John, 2014); particularly since centralized anti-rodent campaigns were introduced and popularized in Taiwan starting in the 1980s (Lu et al., 2003). The farming-related factors township and crop type also influenced *rodent attitude*; farmers from Sanyi township that grow vegetables had the lowest attitude scores, whereas the participants from Zhuolan that grow fruit had the highest scores. As expected, farmers that reported dual problems due to rodents also had the most negative attitudes toward the pest. It is not surprising that these three farming-related behaviors (township, crop type, rodent problem) all had effects on *rodent attitude* since they were also found to be strongly associated with one another. For instance, farmers from Sanyi who grow vegetables were likely to have dual rodent problems for their crops. Therefore, these parameters that reflect personal or community-level experiences would likely contribute to negative attitudes toward wildlife that are problematic and threaten one's livelihood. Personal experiences can be powerful drivers for emotions and perceptions of wildlife that can outweigh objectivity (Slagle et al., 2012;

Castillo-Huitrón et al., 2020), expressly when the context of the experience is conflictive (Inskip & Zimmerman, 2009; Jacobs, 2012; Best & Pei, 2020).

Estimated crop losses were not correlated with the variable *rodent attitude*. A reason for this result could be that the participants estimated annual crop losses due to all pests, not just rodents. Moreover, several farmers ranked fungi as the worst pest for their crops, so if other types of pests are more damaging towards their crops the farmers' attitudes toward rodents may not be as prejudiced or driven by conflictive experiences.

One-third of the farmers in this survey responded that they currently apply rodenticides as a control measure for the pest. Roughly the same proportion of participants claimed to use traps as a means for control. In addition to ARs, traps are commonly utilized in efforts to prevent damage to crops and infrastructure (Singleton, 1999; Meerburg et al., 2008). However, in the current study, farmers who use rodenticides were not more likely to use traps, which could possibly be due to the participants using traps around their houses and not just near their crops or possessing a disinterest in using ARs. The most common response for acquisition of rodenticides was requesting from the government and being supplied the product for free. Additionally, the most common consideration for which product of AR to use was availability, which indicates that rodenticide use behaviors of farmers, such as specific products used, may be influenced in part by government agencies and their recommendations. This would suggest that many of the rodenticides in use would be SGARs, as those are commonly provided by the government presently (Hong et al., 2018). The implications of government-endorsed rodenticide programs (i.e. providing ARs for free), even if operating on a more limited capacity (Hong et al., 2018), could be continual use and application of these control products. However, other methods of

procurement should not be disregarded, and thus, the use of other types of ARs including registered FGARs, since farmers in this survey reported they also purchase rodenticides independently.

Among the farmers that do not currently use rodenticides, many based this decision on the perception that rodenticides are ineffective. There is mounting evidence that supports this opinion (Bedoya-Perez et al., 2019). For example, studies have found that rodents have developed resistance to certain FGARs and SGARs (Lund, 1984; Quy et al., 1995; Meerburg et al., 2008; Buckle, 2013). Concomitantly, individuals or even species of rodents may exhibit neophobia towards the bait or aversive conditioning through associative learning of the taste of the bait and its effects (Prakash, 1988; Inglis et al., 1996; Bedoya-Perez et al., 2019).

Only farming-related factors were found to be important explanatory variables for *rodenticide use*. Farmers from the township Sanyi who also mainly grow vegetables were most likely to use rodenticides. Even though the highest proportion of farmers in this survey ranked rodents as the worst pest for rice, many participants that grow vegetables still reported both singular and dual problems due to rodents. Additionally, some of the rice farmers noted that they practice environmentally-friendly techniques for pest management. Incidentally, the proportion of rice farmers that use rodenticides as a control measure in this study (31.4%) is similar to other studies that have surveyed rice farmers concerning rodent management practices in Asia (Brown & Khamphoukeo, 2010; Brown et al., 2008; Stuart et al., 2011). Unsurprisingly, *worst pest* and *extent of rodent problem* were important factors governing rodenticide use practices; farmers that ranked rodents as the worst and had dual problems were more likely to use rodenticides. These two independent variables

could reflect a proxy for conflictive farming experiences, which would be important determinants for decision-making of pest control practices. Tomass et al. (2020) found that farmer personal experience was the major factor for type of rodent management employed. In the present study, the significant association between *rodenticide use* and *extent or rodent problem* may indicate reactive responses for rodent management; applying rodenticides after crop damage has become visible. Similar KAP studies have found this to be the case – farmers based their rodent control practices on observed crop damage (Singleton, 2003; Brown et al., 2008; Stuart et al., 2011; Tomass et al., 2020). However, further research addressing the stage at which farmers apply rodenticides will be necessary to confirm if rodent management is symptomatic in this agricultural area of Taiwan.

The use of pesticides was much more common among the farmers in the survey; more than double the proportion of farmers who stated they use rodenticides. One probable reason for this finding is the broad definition for ‘pesticide’ utilized in this survey, incorporating insecticides, herbicides, and fungicides. Additionally, since many of the participants were fruit farmers with extensive fungal problems for their crops, the need to apply fungicide would be understandably high. This also likely explains the significant association between *pesticide use* and the explanatory variables *worst pest* and *extent of fungi problem*. Fruit rot due to fungi can cause considerable damage to fruit crops with substantial economic losses (Ann et al., 1999; Byrde & Willetts, 2013). The present study along with several others highlights that pests can be crop specialists or generalists (Hill, 2008; Savary et al., 2019), hence, management strategies may require the use of multiple products.

Education and farming experience (number of years farming) were also associated with *pesticide use*. Farming experience and formal education of the participants were also negatively correlated, so less experienced (younger) farmers with more formal education were less likely to use pesticides. This result is consistent with other wildlife management research, where higher educated individuals are more likely to support ecological and conservation initiatives (Gifford & Nilsson, 2014; Mkonyi et al., 2017; Best & Pei, 2020). This subset of participants in the present study claimed to not use pesticides for environmental protection, therefore, it is likely that they already practice environmentally-friendly farming.

Attitudes toward rodents were linked to rodenticide use. Participants with negative attitudes toward rodents were more likely to apply rodenticides for management. It is well-established that human behavior is associated with attitudes, and this can be heightened in wildlife management contexts (Manfredo et al., 1995; Meerburg et al., 2008; Dickman, 2010). In this study, there is evidence of a causal network between farming-related experiences, attitudes, and certain pest control behaviors (hypothesized in Figure 4.1). As mentioned above, many rodent management responses have been identified as reactive in Asia (Singleton, 2003; John, 2014; Krijger et al., 2017), which could help affirm that experiential factors motivate attitudes and directly or indirectly facilitate pest control practices. These experiential factors would be derived from conflictive scenarios of rodents damaging crops resulting in crop loss and posing a risk to human health. Therefore, successful campaigns for shifts in pest management to more environmentally-friendly practices would need to provide favorable incentives for the stakeholders.

The results of the survey from this study have highlighted areas where non-target wildlife may be especially at risk to chemical poisoning. Vegetable and rice farmers were more likely to use rodenticides, particularly in the township Sanyi. Additionally, farmers perceived rodents to be more problematic for rice and vegetable crops, which could represent high rodent activity in these modified habitats. Rodents like the lesser ricefield rat (*Rattus losea*) and striped field mouse (*Apodemus agararius*) have been recorded to be prolific pests of crops including leafy vegetables, sweet potato, and rice in western Taiwan (Ku & Lin, 1980; Adler, 1995). These two species are common items of a leopard cat's diet (Chuang, 2012) and are distributed throughout Miaoli County (I.N. Best, unpublished data). Rodent specimens from Miaoli County have also been tested for the presence of rodenticides and pesticides. Samples of hair, liver, intestine, and stomach were assayed for concentrations of the chemical products, and hair samples were frequently found to have traces of pesticides, specifically insecticides (K.J.C. Pei, unpublished data). These results support the propensity of rodent exposure to pesticides through dermal contact, and illuminate the potential risk of secondary intoxication of pesticides for predators of rodents. Moreover, the same researchers (K.J.C. Pei, unpublished data) detected concentrations of an FGAR (coumatetralyl) and four SGARs (brodifacoum, bromadiolone, difenacoum, flocoumafen) in liver samples, as well as insecticides in stomach samples from leopard cat specimens that were collected in Miaoli County. Therefore, in addition to secondary intoxication of rodenticides, leopard cats and other non-target wildlife face threats of poisoning of pesticides due to their widespread application, which was reported by farmers in the present study. Secondary poisoning from chemical pest products can have detrimental neurological and behavioral effects (Brakes & Smith, 2005). In order to help

protect non-target wildlife, especially the endangered leopard cat, alternatives to moderate the use of chemical-based pest control should be explored, such as ecologically-based pest management (EBPM). EBPM aims to develop control strategies centered on the ecology and biology of the pest (Singleton et al., 1999). However, effective execution of this will require the compliance and support of stakeholders, the farmers.

Among the farmers who stated they currently use rodenticides and pesticides, many were found to be willing to reduce their usage and application. However, far less participants were willing to stop using rodenticides and pesticides altogether; less than one-quarter for each. The least opposition to stop using rodenticides and pesticides was from participants who grow vegetables and reside in Sanyi. Additionally, a higher proportion of participants whose main source of income is not from farming were more willing to stop using rodenticides. Based on the sample of participants, the main crop grown in Sanyi was vegetables, and over a third of the farmers' main income was not from farming (higher than the two other townships). The main industry of Sanyi is not agriculture, but rather wood carving and tourism, and farming is practiced more recreationally (Miaoli County Government, 2020). Therefore, if farming is practiced in a more recreational capacity removing the strict demands for high crop yields (Zasada, 2011), farmers may be more inclined to operate on an environmentally-friendly basis (Bagheri et al., 2019).

More than half of the participants using rodenticides thought they were effective, and almost three-quarters agreed pesticides were effective. These perceptions of the efficacy of the chemical-based pest products may influence the farmers' decisions to change their pest control behavior, specifically to stop using the products. If a farmer's intention is to maximize their crop yield, they may be less motivated to give up or even modify practices

they perceive promotes productivity (Bagheri et al., 2019). Although other studies have reported that pest management should be multifaceted to be most effective, not just relying on chemical-based solutions, based on farmers' responses from surveys (Brown et al., 2008; Flor & Singleton, 2011; Stuart et al., 2011). In the present study, farmers provided feedback for incentives to change the amount of rodenticides and/ or pesticides they apply. Environmental protection, protecting other people's health, and protecting personal health were among the most popular incentives for changes to both rodenticide and pesticide usage. These findings imply that the farmers in Miaoli County are concerned about the health of their environment, community, and person. Therefore, a strategy to increase support for a reduction of chemical-based pest management could be to further educate the farmers on the ecological hazards associated with the products, namely the adverse impacts on non-target wildlife (Flor & Singleton, 2011). These educational campaigns could also introduce a platform for integrating EBPM. The government resources and support networks that are already established for farmers in Taiwan (COA, 2020) could also help promote awareness of EBPM with relevant educational guides on the ecological factors of pests. Ecologically-based rodent management (EBRM) has been found to be effective in preventing crop damage in other parts of Asia (Singleton et al., 2005; Brown & Khamphoukeo, 2010; Jacob et al., 2010; Palis et al., 2011). Therefore, with proper design and training, the adoption of EBPM could be beneficial for sustainable agriculture and wildlife conservation.

Despite the many insightful findings of this study, there are some limitations and areas where further research would be greatly advantageous. Due to the structured design of the questionnaire, more in-depth and detailed responses were somewhat restricted, particularly

with how pests afflict crops and the methodology for application of pest management. There were several sections in the questionnaire, though, that requested and encouraged participants to expand on their responses, but in some cases these questions were overlooked. Additionally, because I could not oversee all participants complete the questionnaire, some issues with truthfulness or quality control of the responses may exist. However, the questionnaire was designed to not be too sensitive in nature and to not invoke falsification of responses (Nuno & St. John, 2015). In addition, I employed a strict review of the returned questionnaires during the data cleaning stage and, for instance, if there were too many missing responses or lack of consistency these questionnaires were excluded from the sample for analysis. The current study has established areas and conditions where rodents are more prolific as pests, so future studies could focus on these agricultural profiles and carry out in-person interviews with open-ended questions to determine a more comprehensive framework of control behaviors and the feasibility for ecologically-based alternatives.

## **Conclusions**

To date, the relationship between behaviors of farmers for pest control management and risk factors for wildlife in Taiwan remain relatively unexplored. This study highlights the role of rodents in various agricultural environments with particular attention on the extent of damage they inflict. Rodents were perceived to be important pests in the Miaoli agricultural area, especially for the crops rice and vegetables. As a result, attitudes toward rodents were found to be generally negative, which subsequently contributed to decision-making for rodent management, specifically the use of rodenticides. Moreover, farming-related experiences were strong predictors of farmers' pest control behaviors. The

combination of the widespread use of pesticides and high toxicity of SGARS (Meerburg et al., 2008) poses a critical risk for non-target wildlife, which includes the leopard cat. Although most farmers were opposed to terminating their use of rodenticides and/ or pesticides altogether, there was apparent support for incurring reductions of the chemical products. Farmers appeared to be empathetic to protecting their community and environment from the hazards associated with chemical pest products, and further educational programs and support could incentivize the integration of EBPM.



## Tables

**Table 4.1.** Definitions and coding for predictor variables associated with socio-economic factors and farming practices of participants

<b>Predictor</b>	<b>Definition</b>	<b>Type of variable and coding</b>
Township	Township the participant grows their crops/ location of farm	Nominal. 1 = Sanyi, 2 = Zhuolan, 3 = Yuanli
Age	Age of participant	Ordinal. 1 = 18-25, 2 = 26-35, 3 = 36-45, 4 = 46-55, 5 = 56-65, 6 = 65+
Gender	Gender of participant	Nominal (binary). 1 = Male, 2 = Female
Education	Highest level of education participant has completed	Ordinal. 1 = Elementary school, 2 = Junior high school, 3 = High school, 4 = University/ College, 5 = Graduate studies
Main income	The main source of income for the participant	Nominal (binary). 1 = Farming, 2 = Other
Ownership of farm	Whether a farmer owns their farmland or not	Nominal (binary). 0 = No, 1 = Yes
Farming experience	The number of years a participant has been farming	Ordinal. 1 = 1-10, 2 = 11-20, 3 = 21-30, 4 = 30+
Pets	Whether a participant has pets (dogs and/ or cats)	Nominal (binary). 0 = No, 1 = Yes
Farm animals	Whether a participant keeps livestock and/ or poultry	Nominal (binary). 0 = No, 1 = Yes
Crop type	The main crop grown by farmers grouped into categories	Nominal. 1 = Rice, 2 = Vegetables, 3 = Fruit
Crop storage	Whether a farmer stores their crops before distribution/ sale	Nominal (binary). 0 = No, 1 = Yes
Extent of problem	The extent of problems caused by different types of pests on crops (rodents, insects, fungi)	Ordinal. 0 = None, 1 = Singular (only problematic during growing or storing, not both), 2 = Dual (Problematic during both growing and storing)
Worst pest	The pest farmers perceive as the worst/ causes the most damage to crops	Nominal. 0 = None, 1 = Rodents, 2 = Insects, 3 = Plants, 4 = Fungi, 5 = Other
Use of traps	Whether farmers use any sort of trap for rodents, e.g. live or lethal	Nominal (binary). 0 = No, 1 = Yes

**Table 4.2.** Socio-economic factors of farmers and background information about participants' agricultural practices in four townships of Miaoli County.

Variable	<i>n</i>	%	Variable	<i>n</i>	%
<b>Township</b>	126		<b>Main income</b>	126	
Sanyi	30	23.8	Farming	95	75.4
Zhuolan	54	42.9	Other	31	24.6
Yuanli	42	33.3	<b>Ownership of farm</b>	124 <sup>a</sup>	
<b>Age</b>	120 <sup>a</sup>		Yes	90	72.6
18-25	2	1.7	No	34	27.4
26-35	14	11.7	<b>Farming experience</b>	117 <sup>a</sup>	
36-45	22	18.3	1-10	45	38.5
46-55	21	17.5	11-20	21	17.9
56-65	41	34.2	21-30	21	17.9
65+	20	16.7	30+	30	25.6
<b>Gender</b>	107 <sup>a</sup>		<b>Pets</b>	125 <sup>a</sup>	
Male	72	67.3	Yes	64	51.2
Female	35	32.7	No	61	48.8
<b>Education</b>	123 <sup>a</sup>		<b>Keep farm animals</b>	124 <sup>a</sup>	
Elementary school	16	13.0	Yes	34	27.4
Junior high school	18	14.6	No	90	72.6
High school	45	36.6	<b>Crop type</b>	126	
University/ college	38	30.9	Rice	35	27.8
Graduate studies	6	4.9	Vegetables	24	19.0
<b>Main occupation</b>	126		Fruit	67	53.2
Farming	95	75.4	<b>Crop storage</b>	126	
Other	31	24.6	Yes	97	77.0
			No	29	23.0

Notes: <sup>a</sup> indicates lower total *n* value due to missing data, participants left some questions blank

**Table 4.3.** Chi-square test statistics determining associations between extent of problem of the different pests and independent variables. Significant values are displayed in bold.

Variable	<i>n</i>	<u>Rodent problem</u>			<u>Insect problem</u>			<u>Fungi problem</u>				
		$\chi^2$	<i>df</i>	<i>P</i>	<i>n</i>	$\chi^2$	<i>df</i>	<i>P</i>	<i>n</i>	$\chi^2$	<i>df</i>	<i>P</i>
Township	126	15.84	4	<b>&lt;0.005</b>	126	1.15	4	0.886	126	11.31	4	<b>&lt;0.05</b>
Crop type	126	12.88	4	<b>&lt;0.05</b>	126	1.10	4	0.896	126	15.75	4	<b>&lt;0.005</b>
Crop stor.	126	11.24	2	<b>&lt;0.005</b>	126	2.43	2	0.297	126	10.35	2	<b>&lt;0.01</b>

Notes: Crop stor. = crop storage; <sup>a</sup> indicates lower total *n* value due to missing data, participants left some questions blank.

**Table 4.4.** PCA loading of ‘attitudes toward rodents’ component, mean Likert score, and distribution (%) of agreement of farmers for statements related to attitudes toward rodents

Original statement	<i>Rodent attitude</i> loading score	Mean Likert score (1-5) <sup>a</sup>	% of farmers		
			Agree	Neutral	Disagree
Rodents are a major pest for my house	0.751	2.63	43.3	42.3	14.4
Rodents are a major pest for farming in my community	0.909	2.57	45.8	42.7	11.5
Rodents are a risk to people	0.769	2.24	66.3	28.4	5.3

Notes: <sup>a</sup> Likert scale has been reversed (1 = strongly agree... 5 = strongly disagree) for lower scores to indicate negative attitudes

**Table 4.5.** Separate GLMs between each factor (independent variable) and the dependent variable rodent attitude. Significant values are displayed in bold

Model	Factor	Wald $\chi^2$	df	P
1	Township	7.52	2	< <b>0.05</b>
2	Age	11.26	4	< <b>0.05</b>
3	Gender	0.05	1	0.892
4	Education	2.73	4	0.605
5	Main income	0.45	1	0.504
6	Farming experience	2.43	3	0.489
7	Pets	0.02	1	0.901
8	Farm animals	0.39	1	0.530
9	Crop type	6.39	2	< <b>0.05</b>
10	Crop storage	0.00	1	0.998
11	Worst pest	5.04	2	0.283
12	Rodent problem	10.14	2	< <b>0.01</b>

Notes: Models were run separately for each factor to test the effect with full available data and to avoid influencing the model due to too many missing data values.

**Table 4.6.** Chi-square test statistics determining associations between independent variables and participant rodenticide use, willingness of participants to 'use less rodenticides' and 'stop using rodenticides.' Significance is indicated in bold.

Variable	Rodenticide use				Use less rodenticides				Stop using rodenticides			
	<i>n</i>	$\chi^2$	<i>df</i>	<i>P</i>	<i>n</i>	$\chi^2$	<i>df</i>	<i>P</i>	<i>n</i>	$\chi^2$	<i>df</i>	<i>P</i>
Township	126	7.11	2	<b>&lt;0.05</b>	37 <sup>a</sup>	2.33	4	0.699	37 <sup>a</sup>	9.85	4	<b>&lt;0.05</b>
Age	120 <sup>a</sup>	7.05	5	0.217	33 <sup>a</sup>	5.64	8	0.753	33 <sup>a</sup>	5.20	8	0.805
Gender	107 <sup>a</sup>	0.15	1	0.696	35 <sup>a</sup>	0.36	2	0.900	35 <sup>a</sup>	4.31	2	0.122
Education	123 <sup>a</sup>	3.97	4	0.410	37 <sup>a</sup>	6.88	8	0.596	37 <sup>a</sup>	10.11	8	0.270
Main income	126	1.34	1	0.247	37 <sup>a</sup>	4.44	2	0.117	37 <sup>a</sup>	16.02	2	<b>&lt;0.001</b>
Ownership	124 <sup>a</sup>	0.40	1	0.528	37 <sup>a</sup>	2.54	2	0.281	37 <sup>a</sup>	4.23	2	0.122
Farming experience	117 <sup>a</sup>	4.83	3	0.184	32 <sup>a</sup>	5.23	6	0.566	32 <sup>a</sup>	9.12	6	0.169
Pets	125 <sup>a</sup>	0.15	1	0.701	36 <sup>a</sup>	4.07	2	0.134	36 <sup>a</sup>	1.09	2	0.677
Farm animals	124 <sup>a</sup>	0.00	1	0.989	35 <sup>a</sup>	3.21	2	0.189	35 <sup>a</sup>	1.10	2	0.699
Crop type	126	8.72	2	<b>&lt;0.05</b>	37 <sup>a</sup>	4.72	4	0.332	37 <sup>a</sup>	12.31	4	<b>&lt;0.05</b>
Crop storage	126	2.71	1	0.100	37 <sup>a</sup>	1.05	2	0.796	37 <sup>a</sup>	1.58	2	0.790
Use of traps	117 <sup>a</sup>	3.17	1	0.075	34 <sup>a</sup>	3.29	2	0.226	34 <sup>a</sup>	3.78	2	0.151
Worst pest	126	14.89	4	<b>&lt;0.005</b>	37 <sup>a</sup>	11.94	6	<b>&lt;0.05</b>	37 <sup>a</sup>	9.28	6	0.148
Rodent problem	126	50.79	2	<b>&lt;0.001</b>	37 <sup>a</sup>	0.57	2	0.756	37 <sup>a</sup>	3.28	2	0.246
Insect problem	126	9.02	2	<b>&lt;0.05</b>	37 <sup>a</sup>	1.89	4	0.773	37 <sup>a</sup>	7.10	4	0.143
Fungi problem	126	3.96	2	0.138	37 <sup>a</sup>	2.27	4	0.719	37 <sup>a</sup>	8.17	4	0.086
Plant problem	126	2.29	2	0.382	37 <sup>a</sup>	3.35	4	0.572	37 <sup>a</sup>	3.54	4	0.509

Notes: <sup>a</sup> indicates lower total *n* value due to missing data, participants left these questions blank

**Table 4.7.** Chi-square test statistics determining associations between independent variables and participant pesticide use, willingness of participants to ‘use less pesticides’ and ‘stop using pesticides.’ Significance is indicated in bold.

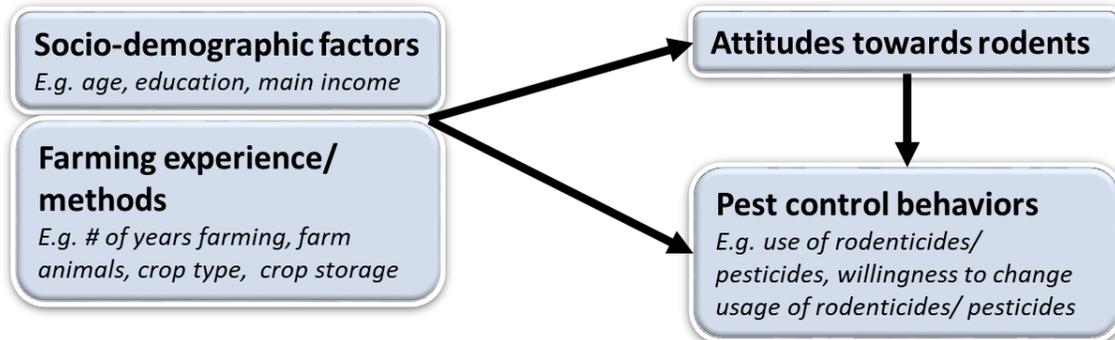
Variable	Pesticide use				Use less pesticides				Stop using pesticides			
	<i>n</i>	$\chi^2$	<i>df</i>	<i>P</i>	<i>n</i>	$\chi^2$	<i>df</i>	<i>P</i>	<i>n</i>	$\chi^2$	<i>df</i>	<i>P</i>
Township	125 <sup>a</sup>	6.48	2	<b>&lt;0.05</b>	93 <sup>a</sup>	9.47	4	0.050	93 <sup>a</sup>	20.37	4	<b>&lt;0.001</b>
Age	119 <sup>a</sup>	7.23	5	0.208	87 <sup>a</sup>	18.01	10	0.050	87 <sup>a</sup>	10.52	8	0.409
Gender	106 <sup>a</sup>	0.28	1	0.596	78 <sup>a</sup>	6.70	2	<b>&lt;0.05</b>	78 <sup>a</sup>	13.10	2	<b>&lt;0.005</b>
Education	122 <sup>a</sup>	18.74	4	<b>&lt;0.005</b>	91 <sup>a</sup>	5.42	8	0.730	91 <sup>a</sup>	5.29	8	0.750
Main income	125 <sup>a</sup>	3.55	1	0.060	93 <sup>a</sup>	1.81	2	0.430	93 <sup>a</sup>	1.67	2	0.434
Ownership	123 <sup>a</sup>	0.13	1	0.722	91 <sup>a</sup>	0.28	2	0.870	91 <sup>a</sup>	1.70	2	0.428
Farming experience	116 <sup>a</sup>	8.33	3	<b>&lt;0.05</b>	85 <sup>a</sup>	7.11	6	0.319	85 <sup>a</sup>	4.27	6	0.657
Pets	124 <sup>a</sup>	1.11	1	0.292	92 <sup>a</sup>	3.42	2	0.181	92 <sup>a</sup>	3.33	2	0.189
Farm animals	123 <sup>a</sup>	0.06	1	0.804	91 <sup>a</sup>	5.07	2	0.103	91 <sup>a</sup>	4.39	2	0.111
Crop type	125 <sup>a</sup>	1.53	2	0.466	93 <sup>a</sup>	8.85	4	0.063	93 <sup>a</sup>	11.39	4	<b>&lt;0.05</b>
Crop storage	125 <sup>a</sup>	0.58	1	0.445	93 <sup>a</sup>	0.24	2	0.933	93 <sup>a</sup>	0.27	2	0.874
Use of traps	117 <sup>a</sup>	0.68	1	0.411	85 <sup>a</sup>	0.47	2	0.790	85 <sup>a</sup>	3.31	2	0.191
Worst pest	125 <sup>a</sup>	31.76	4	<b>&lt;0.001</b>	93 <sup>a</sup>	7.73	6	0.257	93 <sup>a</sup>	10.27	6	0.107
Rodent problem	125 <sup>a</sup>	2.84	2	0.241	93 <sup>a</sup>	14.90	4	<b>&lt;0.005</b>	93 <sup>a</sup>	6.45	4	0.168
Insect problem	125 <sup>a</sup>	1.11	2	0.575	93 <sup>a</sup>	1.41	4	0.855	93 <sup>a</sup>	1.96	4	0.761
Fungi problem	125 <sup>a</sup>	15.29	2	<b>&lt;0.001</b>	93 <sup>a</sup>	4.18	4	0.395	93 <sup>a</sup>	4.33	4	0.375
Plant problem	125 <sup>a</sup>	0.29	2	0.863	93 <sup>a</sup>	6.79	4	0.102	93 <sup>a</sup>	0.93	4	0.921

Notes: <sup>a</sup> indicates lower total *n* value due to missing data, participants left these questions blank

**Table 4.8.** Distribution of agreement for farmers' willingness to change pest control behaviors based on significant independent variables (Table 6, 7)

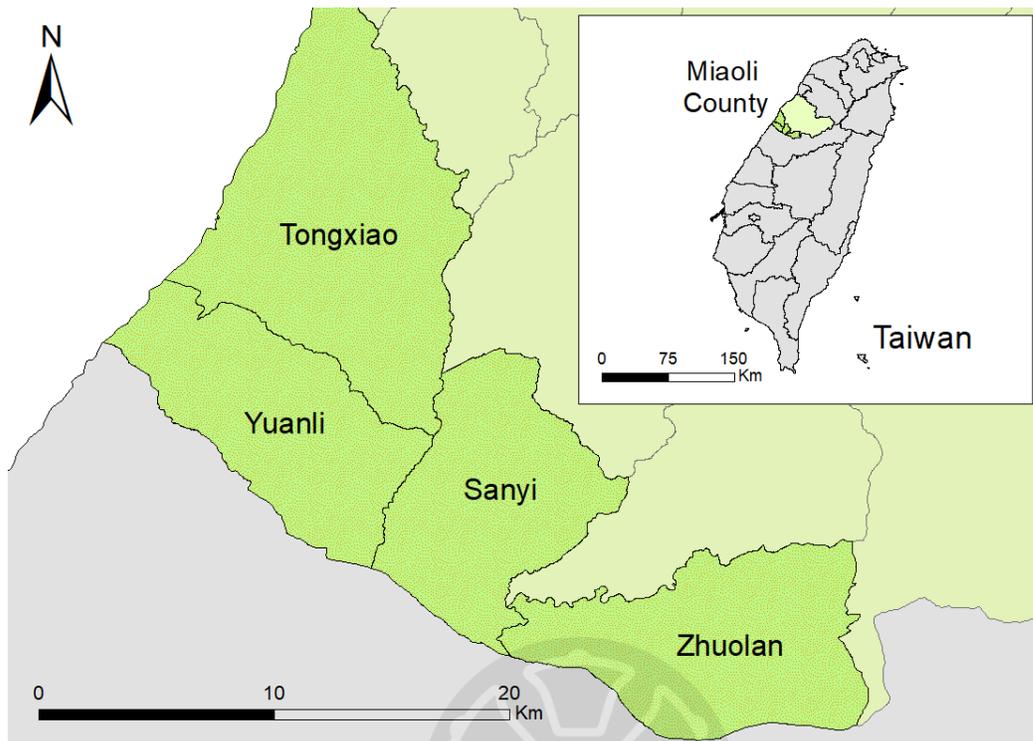
Behavior	Variable	n	% of farmers		
			Disagree	Neutral	Agree
Use less rodenticides	Worst pest	37	24.4	29.7	45.9
	<i>Rodents</i>	14	0.0	50.0	50.0
	<i>Insects</i>	11	27.3	18.2	54.5
	<i>Fungi</i>	11	45.4	18.2	36.4
	<i>Other</i>	1	100.0	0.0	0.0
Stop using rodenticides	Township	37	51.4	24.3	24.3
	<i>Sanyi</i>	14	21.4	42.9	35.7
	<i>Zhuolan</i>	13	76.9	15.4	7.7
	<i>Yuanli</i>	10	60.0	10.0	30.0
	Main income	37	51.4	24.3	24.3
	<i>Farming</i>	29	65.5	24.1	10.3
	<i>Other</i>	8	0.0	25.0	75.0
	Crop type	37	51.4	24.3	24.3
	<i>Rice</i>	10	60.0	10.0	30.0
	<i>Vegetables</i>	13	15.4	46.1	38.5
Use less pesticides	<i>Fruit</i>	14	78.6	14.3	7.1
	Gender	77	13.0	24.7	62.3
	<i>Male</i>	53	17.0	17.0	66.0
	<i>Female</i>	24	4.2	41.6	54.2
	Rodent problem	93	14.0	20.4	65.6
	<i>None</i>	40	5.0	12.5	82.5
	<i>Singular</i>	29	31.0	24.1	44.8
Stop using pesticides	<i>Dual</i>	24	8.3	29.2	62.5
	Township	93	52.7	28.0	19.4
	<i>Sanyi</i>	25	16.0	52.0	32.0
	<i>Zhuolan</i>	42	71.4	16.7	11.9
	<i>Yuanli</i>	26	57.7	23.1	19.2
	Gender	77	48.1	32.5	19.4
	<i>Male</i>	53	60.4	20.7	18.9
	<i>Female</i>	24	20.8	58.3	20.8
	Crop type	93	52.7	28.0	19.3
	<i>Rice</i>	25	48.0	28.0	24.0
<i>Vegetables</i>	16	18.7	50.0	31.3	
<i>Fruit</i>	52	65.4	21.1	13.5	

## Figures

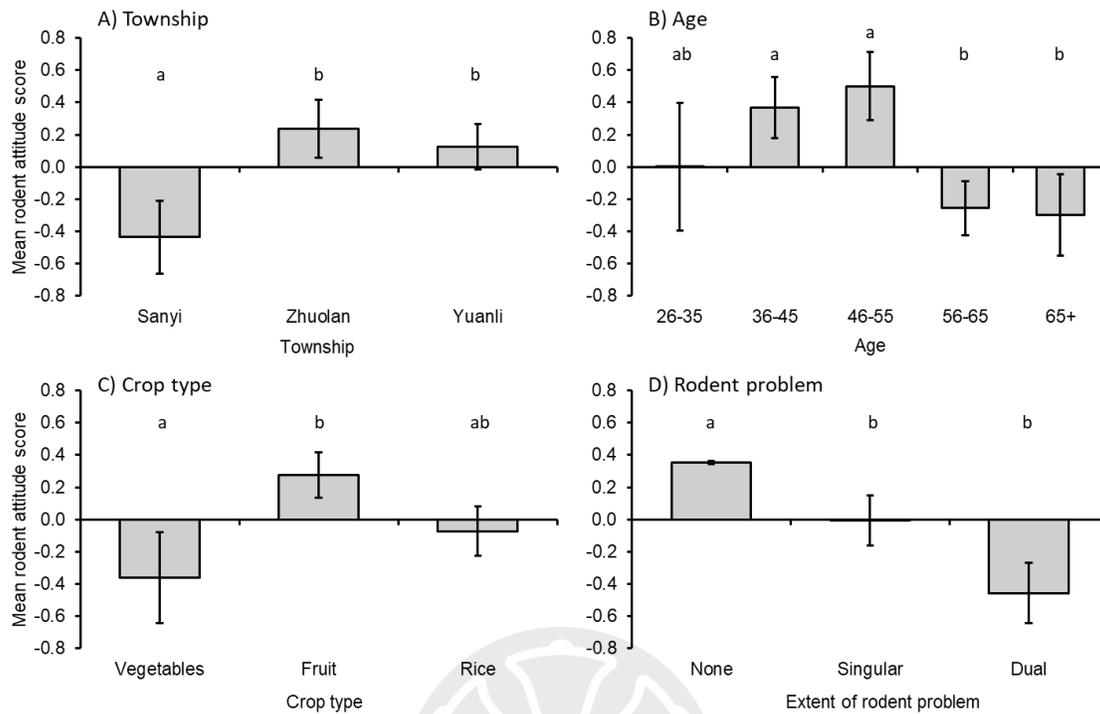


**Figure 4.1.** Schematic of conceptual framework for associations between different parameters of farmers from the survey ( $N = 126$ ). Both ‘socio-economic factors’ and ‘farming experience’ delineated as independent variables. Arrows indicate explanatory power/ influence.

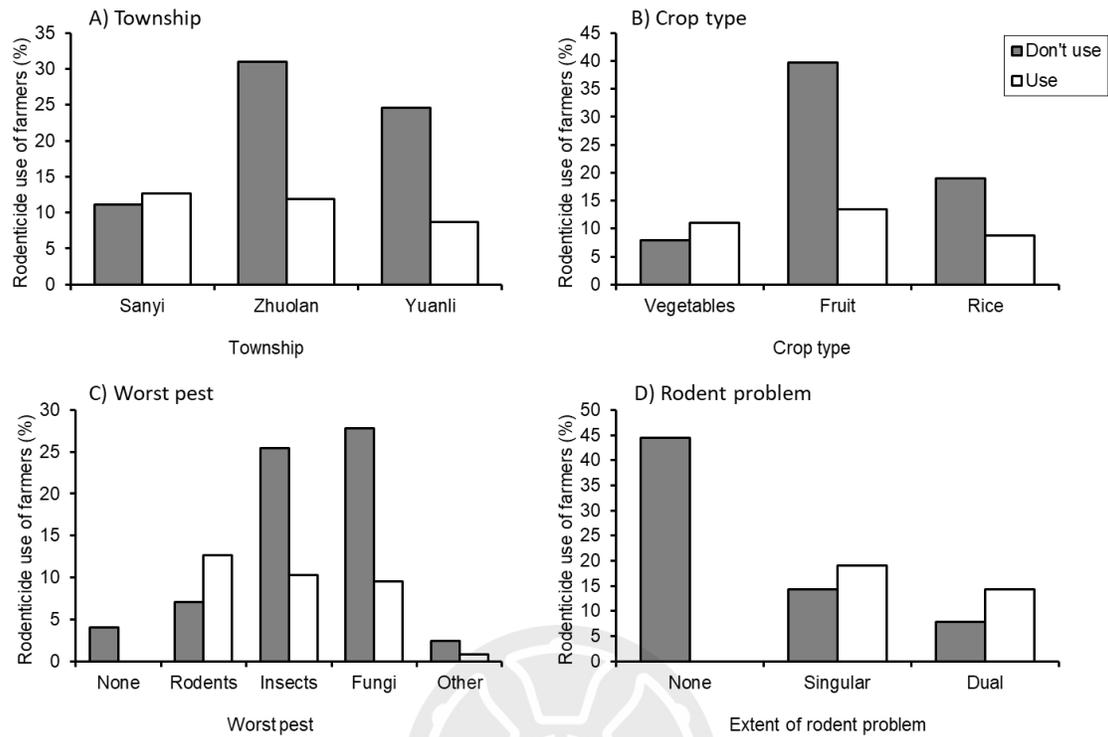




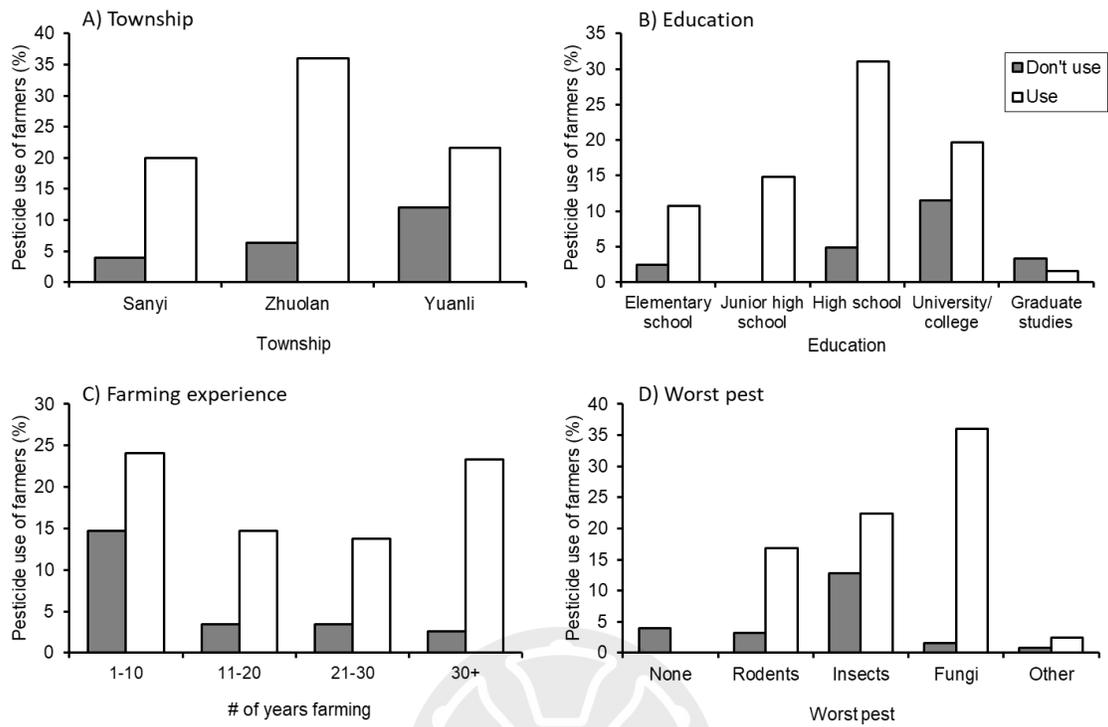
**Figure 4.2.** Map of townships Zhuolan, Sanyi, Yuanli, and Tongxiao in Miaoli County, Taiwan, where sampling for the survey was conducted.



**Figure 4.3.** Mean rodent attitude scores of participants compared between A) township, B) age, C) crop type, and D) extent of rodent problem. Negative values indicate negative attitudes, and positive values indicate positive attitudes. Error bars represent standard error of the mean.



**Figure 4.4.** Rodenticide use of farmers (%) compared between A) township, B) crop type, C) worst pest, and D) extent of rodent problem, from participants of survey in Miaoli County.



**Figure 4.5.** Pesticide use of farmers (%) compared between A) township, B) education, C) farming experience, and D) worst pest, from participants of the survey in Miaoli County.

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## **Chapter 5: General conclusions and future work**

### **Lack of responses to predator odors**

A consistent finding in both studies described in chapters 2 and 3 was the lack of predator odor effects on inducing defensive behaviors. An explanation for the lack of responses from the rodents in eastern Taiwan (chapter 2) was the possibility of naivety – the rodents are unable to discriminate leopard cat odors due to no prior encounters, following the naivety hypothesis (Carthey & Blumstein, 2018). However, the results from the field study in Miaoli (chapter 3) indicate that the predator odors largely had no effect on rodent foraging behavior. Both leopard cats and domestic cats have been documented in my study area in Miaoli County, so it is unlikely that the rodents observed during this study are naïve to the predator odors. The results presented in both chapters 2 and 3 are consistent with other predation risk studies that have been conducted in both laboratory (Bramley & Waas, 2001; Apfelbach et al., 2005; Cremona et al., 2015; Jolly et al., 2018) and field (Pusenius & Ostfeld, 2002; Orrock et al., 2004; Spencer et al., 2014; Stryjek et al., 2018) conditions. Therefore, other parameters may be more important in governing behavior and decision-making of prey in theoretically risky contexts, such as behavioral traits.

### **Behavioral variation between individuals and species**

This thesis provides empirical evidence of the link between behavior and POL at an inter-specific level in both laboratory and field settings. In the study described in chapter 2, not only was inter-specific behavioral variation demonstrated, but also between-individual variation. The smaller, “faster” mice species exhibited a higher proportion of non-defensive

behaviors, whereas the larger, “slower” rat species exercised more caution in the novel microenvironment. Concomitantly, based on the repeatability analysis, individuals were generally consistent in most behaviors, which suggests intra-specific variation (Réale et al., 2007; Martin & Réale, 2008; Dammhahn et al., 2018). For example, some individuals may be bolder than others and rates of exploration may vary between individuals.

The field study described in chapter 3 presents novel findings of inter-specific variation in behavioral responses of rodents to risk in their natural habitat, which adhere to a fast-slow continuum and reinforce the connection between behavior and POL. Once again, the larger rat species exercised more caution and vigilance to the foraging stations, and the smaller mouse species performed a higher proportion of behaviors reflecting boldness. Although it was not tested for the purposes of this thesis, it is possible that the populations of rodents in Miaoli also embody between-individual behavioral variation. Further work will need to be carried out to substantiate intra-specific differences.

It is possible that the existence of behavioral variation between individuals and species may overshadow any deterrent effect of predator odors or other risk cues (Réale et al., 2007; Cremona et al., 2015; Garvey et al., 2020). For instance, when comparing between species, those that are shorter-lived may take more risks and prioritize current reproduction opportunities, and those that have longer life spans may take less risks to optimize their survival (Sih et al., 2004; Wolf et al., 2007; Montiglio et al., 2018). Thus, at the community level some species may respond to risk cues and others may not. When focusing on a single species, between-individual variation may result in exceptionally bold individuals that offset the ‘average’ response and mask predator odor effects (Martin & Réale, 2008;

Cremona et al., 2015; Garvey et al., 2020). However, certain risk cues may pose too high a risk for even the boldest individuals.

### **Indirect cues for predation risk**

Despite the lack of responses to predator odors in the field experiment in Miaoli (chapter 3), rodent foraging behavior was strongly influenced by the indirect cue microhabitat variation. Foraging activity, measured via seed consumption, was significantly lower at experimental food patches that were exposed and devoid of vegetation cover. Comparable results have been reported in several other similarly designed studies (Pusenius & Ostfeld, 2002; Orrock et al., 2004; Orrock & Danielson, 2004; Verdolin, 2006). It is possible that the avoidance of exposed microhabitat by rodents is a proactive approach to avoid areas of high risk that represent a constant in the landscape of fear (Lima & Dill, 1990; While & McArthur, 2006; Gaynor et al., 2019). This avoidance behavior may be even more pronounced when rodents face predation pressure from avian, reptilian, and mammalian taxa. Rodent-eating raptors have been observed in my study area in Miaoli (chapter 3), so rodents may perceive cues associated with avian predation as high risk.

### **Agricultural profiles for rodent problems**

Based on the farmers' responses from the survey described in chapter 4, rodents were the most prolific pests for the crop rice and in the township Sanyi. Rodents are widely considered to be major pests for rice production across Asia (Singleton, 2003; Brown et al., 2008; Stuart et al., 2011). Nevertheless, farmers also perceived rodents to be problematic for leafy vegetables and in the township Yuanli. Concurrently, farming-related and

experiential factors (e.g. crop type, township, extent of rodent problem) were important predictors for both rodenticide and pesticide use. A strong relationship was found between the factors township, crop type, extent of problem, attitudes toward rodents, and rodenticide use. For instance, farmers that suffered more crop damage due to rodents, such as rice farmers, were more probable to have negative attitudes towards rodents and apply rodenticides, likely following a reactive approach that is common to rodent management in Asia (Singleton et al., 1999; John, 2014; Tomass et al., 2020). Uncovering agricultural profiles that characterize rodent-inflicted damage and the symptomatic pest control measures also has implications for risks to non-target wildlife. Modified habitat that is perceived to be resource-rich by rodents, such as fields of crops, may also have a greater chance of ARs deployed. Therefore, for non-target wildlife that predate on rodents, such as the leopard cat, these areas could exemplify high risk for secondary exposure to the poisons (Rattner et al., 2014; López-Perea & Mateo, 2018). In order to help mitigate these threats alternatives for pest control should be explored.

### **Applications of landscape of fear for pest management**

In the survey described in chapter 4, farmers were found to be supportive towards reducing their usage of chemical pest control products. These participants also indicated awareness and consideration for the protection of the environment and their respective communities. Therefore, integrating EBPM that incorporates the landscape of fear framework could provide a solution.

According to the results of the study conducted in Miaoli County (chapter 3), the application of predator odors to deter rodents from foraging at food patches may not be the

most effective. The manipulation of perceived predation risk with the use of direct cues failed to represent dangerous areas where the risks outweighed the rewards. In this study system, the landscape of fear was more accurately defined by microhabitat characteristics – exposed areas reflecting high risk due to lack of vegetation cover, limited escape routes, and threats from avian predators. As mentioned above, microhabitat has been found to be a strong indirect cue of risk eliciting antipredator behaviors, hence, the application of this cue for pest management could be worthwhile. The strategic placement of traps and/ or lures in microhabitat type where there is expected to be more rodent activity could be an effective measure (Krijger et al., 2017). For example, Jones et al. (2017) found that in an agricultural area of the Philippines *Rattus tanezumi* was more likely to visit baits and traps placed in the center of rice fields with more dense vegetation compared to the perimeter. Creating obstacles in the landscape surrounding cropland could be a deterrent, in a survey conducted by Brown & Khamphoukeo (2010) farmers reported that they perceived digging ditches and burrows surrounding their rice crops to be an effective control strategy for rodents.

The ultimate goal for implementing the predation risk framework toward pest management is to elicit antipredator behavioral responses so pests avoid certain areas thereby alleviating crop damage. The combination of direct risk cues has been found to instigate antipredator responses in a variety of systems (Bedoya-Perez et al., 2019; Moll et al., 2020). For instance, the combination of visual and olfactory stimuli could simulate high, apparent predation risk for rodents, as was reported by Moll et al. (2020). Predator models/ decoys and odors are becoming more readily available (Moll et al., 2020) with commercial retailers providing global distribution (e.g. PredatorPee® Inc – predator odors; Bird-X™ -

predator models and decoys). Auditory cues have also had success in deterring prey species and inducing defensive behaviors (Suraci et al., 2016; Suraci et al., 2017; Lyly et al., 2018). Suraci et al. (2017) developed a motion sensor audio playback system that is triggered when animals approach, which would reflect immediate danger for any prey individual. In the study system in Miaoli, visual stimuli resembling a raptor species paired with audio playback of the raptor species could be an efficient strategy.

In addition to manipulation of predation risk to deter rodents from pest-related activities, the recruitment of the actual predators to facilitate both consumptive and non-consumptive effects on rodents would also be a beneficial tool for not only pest management, but biodiversity conservation. For instance, developing artificial perches for raptor species could be a cost-effective and straightforward approach for recruiting birds of prey and increasing the predation rates on rodent pests (Hall et al., 1981; Krijger et al., 2017). Additionally, further educating the local communities in the agricultural areas of Miaoli on the relative importance of predators, such as leopard cats, for regulating populations of rodents (providing biological control) could also be advantageous.

Tackling pest problems is a challenging endeavor, contemporary management should follow a holistic approach. The importance of behavioral variation between species, populations, and individuals of pests should not be overlooked because not all motivations will be equal (Garvey et al., 2020). Regardless of what specific strategies or predation risk cues are considered, further work addressing the efficacy, as well as ecological, economical, and logistical constraints will be necessary.

## Future work

The work in this thesis provides novel insights towards the roles of rodents in Taiwan, from their behavioral responses to simulated risk to their contribution as pests in agriculture. The work presented in chapters 2 and 3 highlights the significance of both inter- and intra-specific behavioral variation in different contexts. More specifically, how individuals belonging to the same species can embody behavioral traits, or “personalities”, resulting in differential responses to risky situations. In chapter 2, which covers Best et al. (2020), an initial assessment of intra-individual behavioral consistency was carried out. Thus, future research could adopt a more robust methodology aligning to animal personality research with integration into a multi-species comparative design that reinforces behavioral types, as well as inter-specific differences linking behavior to POL. This methodological framework could be applied to both laboratory and field studies. The latter type of study, which could be achieved by tagging individuals with RFID chips, could underpin how individual variation may offset species- and community-level responses to risk cues (Gaynor et al., 2019; Garvey et al., 2020). However, other types of direct risk cues, such as visual or auditory, should also be applied in field studies to test the magnitude of effect, and whether “bold” individuals or “fast” species will still take risks for a reward. The results of such studies could then further develop a predation risk framework and determine its feasibility to be implemented in pest management. Finally, future research should focus on surveying the agricultural profiles presented in chapter 4 where pest rodents are most pervasive and non-target wildlife are most at risk to establish a basis for support from stakeholders to introduce elements of EBPM.

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## Appendices

### Appendix A: Supplementary material for Chapter 2

#### Tables

**Table S2.1.** Spearman rank correlation matrix of all measured individual behaviors. Significant values are displayed in bold.

	Expl.	For.	Mot.	Conc.	Groom.	Cons. R.	For. Ev.	Lat. For.	Jump.
Expl.	1	-0.621 <b>&lt;0.001</b>	0.088 0.310 <b>&lt;0.001</b>	-0.065 0.450 <b>&lt;0.001</b>	0.284 <b>&lt;0.001</b>	-0.504 <b>&lt;0.001</b>	-0.148 0.085 <b>&lt;0.001</b>	0.460 <b>&lt;0.001</b>	0.765 <b>&lt;0.001</b>
For.	-0.621 <b>&lt;0.001</b>	1	-0.235 <b>&lt;0.01</b>	-0.319 <b>&lt;0.001</b>	-0.335 <b>&lt;0.001</b>	0.875 <b>&lt;0.001</b>	0.613 <b>&lt;0.001</b>	-0.838 <b>&lt;0.001</b>	-0.580 <b>&lt;0.001</b>
Mot.	0.088 0.310 <b>&lt;0.01</b>	-0.235 <b>&lt;0.01</b>	1	-0.384 <b>&lt;0.001</b>	0.478 <b>&lt;0.001</b>	-0.242 <b>&lt;0.01</b>	-0.129 0.133 <b>&lt;0.05</b>	0.209 <b>&lt;0.05</b>	0.038 0.660
Conc.	-0.065 0.450 <b>&lt;0.001</b>	-0.319 <b>&lt;0.001</b>	-0.384 <b>&lt;0.001</b>	1	-0.208 <b>&lt;0.05</b>	-0.255 <b>&lt;0.005</b>	-0.199 <b>&lt;0.05</b>	0.245 <b>&lt;0.005</b>	0.103 0.231
Groom.	0.284 <b>&lt;0.001</b>	-0.335 <b>&lt;0.001</b>	0.478 <b>&lt;0.001</b>	-0.208 <b>&lt;0.05</b>	1	-0.264 <b>&lt;0.005</b>	-0.184 <b>&lt;0.05</b>	0.311 <b>&lt;0.001</b>	0.268 <b>&lt;0.005</b>
Cons. R.	-0.504 <b>&lt;0.001</b>	0.875 <b>&lt;0.001</b>	-0.242 <b>&lt;0.01</b>	-0.255 <b>&lt;0.01</b>	-0.264 <b>&lt;0.005</b>	1	0.717 <b>&lt;0.001</b>	-0.842 <b>&lt;0.001</b>	-0.476 <b>&lt;0.001</b>
For. Ev.	-0.148 0.085 <b>&lt;0.001</b>	0.613 <b>&lt;0.001</b>	-0.129 0.133 <b>&lt;0.05</b>	-0.199 <b>&lt;0.05</b>	-0.184 <b>&lt;0.05</b>	0.717 <b>&lt;0.001</b>	1	-0.729 <b>&lt;0.001</b>	-0.270 <b>&lt;0.005</b>
Lat. For.	0.460 <b>&lt;0.001</b>	-0.838 <b>&lt;0.001</b>	0.209 <b>&lt;0.05</b>	0.245 <b>&lt;0.005</b>	0.311 <b>&lt;0.001</b>	-0.842 <b>&lt;0.001</b>	-0.729 <b>&lt;0.001</b>	1	0.441 <b>&lt;0.001</b>
Jump.	0.765 <b>&lt;0.001</b>	-0.580 <b>&lt;0.001</b>	0.038 0.660	0.103 0.231	0.268 <b>&lt;0.005</b>	-0.476 <b>&lt;0.001</b>	-0.270 <b>&lt;0.005</b>	0.441 <b>&lt;0.001</b>	1

**Notes:** Expl. = exploring, For. = foraging, Mot. = motionless, Conc. = concealing, Groom. = grooming, Cons. R. = consumption ratio, For. Ev. = foraging events, Lat. For. = latency to forage, Jump. = jumping.

**Table S2.2.** Mean and standard error in duration (sec.), amount (%) and frequency of response behaviors of species and sexes for Trial 1

			<sup>a</sup> Expl.	<sup>a</sup> For.	<sup>a</sup> Mot.	<sup>a</sup> Conc.	<sup>a</sup> Groom.	<sup>a</sup> Def.	<sup>a</sup> Non-def.	<sup>b</sup> Cons.R.	<sup>c</sup> For. Ev.	<sup>a</sup> Lat. For.	<sup>c</sup> Jump.
<i>M. caroli</i>	Male	Mean	1428.20	388.60	208.40	53.40	21.40	261.80	1816.80	0.32	0.40	1327.60	41.20
		S.E.	350.51	384.86	118.64	36.82	7.03	149.81	147.95	0.32	0.24	473.00	25.13
	Female	Mean	1704.00	168.00	24.50	154.38	49.13	178.88	1872.00	0.31	1.75	1567.13	74.88
		S.E.	169.44	139.70	11.71	126.70	14.08	125.39	125.13	0.21	1.08	275.78	22.83
	Total	Mean	1597.92	252.85	95.23	115.54	38.46	210.77	1850.77	0.31	1.23	1475.00	61.92
		S.E.	166.01	164.18	50.21	78.34	9.63	93.04	92.13	0.17	0.68	238.99	17.04
<i>A. agrarius</i>	Male	Mean	625.43	1271.14	29.86	103.86	69.71	133.71	1896.57	2.90	9.14	158.29	0.14
		S.E.	63.89	60.07	13.38	75.90	29.93	73.95	97.81	0.53	1.39	31.57	0.14
	Female	Mean	531.11	1187.22	83.67	261.22	36.78	344.89	1718.33	2.33	5.00	485.56	1.00
		S.E.	79.95	144.32	67.89	172.29	14.92	175.79	168.46	0.54	0.76	139.47	0.88
	Total	Mean	572.38	1223.94	60.13	192.38	51.19	252.50	1796.31	2.58	6.81	342.38	0.63
		S.E.	52.71	83.64	38.23	101.59	15.53	104.69	103.48	0.38	0.89	88.13	0.50
<i>R. exulans</i>	Male	Mean	767.00	591.20	45.53	649.47	46.80	695.00	1358.20	1.37	6.40	867.53	16.80
		S.E.	96.64	142.29	13.66	169.18	22.83	166.90	173.48	0.33	1.43	239.99	10.07
	Female	Mean	1006.14	339.43	227.43	438.86	88.14	666.29	1345.57	0.86	2.86	1244.43	29.00
		S.E.	179.93	172.81	107.82	176.53	39.54	178.03	190.36	0.48	1.61	329.22	19.63
	Total	Mean	843.09	511.09	103.41	582.45	59.95	685.86	1354.18	1.21	5.27	987.45	20.68
		S.E.	88.20	112.13	38.52	127.67	19.92	124.70	130.29	0.27	1.14	193.65	9.09
<i>R. losea</i>	Male	Mean	680.00	891.30	388.40	5.90	134.40	394.30	1571.30	1.37	6.00	523.20	15.60
		S.E.	82.96	131.35	107.22	5.37	53.05	106.01	114.59	0.26	0.91	212.89	6.25
	Female	Mean	726.00	24.29	636.43	311.86	401.43	948.29	750.29	0.05	0.14	2075.71	12.86
		S.E.	94.35	24.29	143.88	203.13	66.48	122.05	87.40	0.05	0.14	24.29	11.37
	Total	Mean	698.94	534.29	490.53	131.88	244.35	622.41	1233.24	0.82	3.59	1162.47	14.47
		S.E.	60.70	131.07	89.06	88.31	51.89	103.27	125.41	0.22	0.89	227.10	5.75
<b>Total</b>	Male	Mean	806.05	773.57	157.24	291.76	71.38	449.00	1579.62	1.52	6.00	702.46	16.62
		S.E.	75.31	95.03	40.74	84.67	18.64	83.77	86.91	0.22	0.78	138.22	5.64
	Female	Mean	985.06	470.16	225.68	285.19	133.90	510.87	1455.23	0.96	2.58	1295.10	29.06
		S.E.	105.06	107.47	60.32	82.89	31.73	91.00	105.43	0.25	0.58	150.31	9.08
	Total	Mean	887.66	635.25	188.44	288.76	99.88	477.21	1522.91	1.26	4.44	972.63	22.29
		S.E.	63.48	73.07	35.29	59.15	17.93	61.29	67.34	0.17	0.54	107.23	5.17

**Notes:** Expl. = exploring, For. = foraging, Mot. = motionless, Conc. = concealing, Groom. = grooming, Def. = defensive, Non-def. = non-defensive, Cons.R. = consumption ratio, For. Ev. = foraging events, Lat. For. = latency to forage, Jump. = jumping. <sup>a</sup>Duration-based response (out of 2100 sec.); <sup>b</sup> amount (%); <sup>c</sup> number of occurrences. S.E. = standard error of mean.

**Table S2.3.** Mean and standard error in duration (sec.), amount (%) and frequency of response behaviors of species and treatment groups for Trial 2

			<sup>a</sup> Expl.	<sup>a</sup> For.	<sup>a</sup> Mot.	<sup>a</sup> Conc.	<sup>a</sup> Groom.	<sup>a</sup> Def.	<sup>a</sup> Non-def.	<sup>b</sup> Cons.R.	<sup>c</sup> For. Ev.	<sup>a</sup> Lat. For.	<sup>c</sup> Jump.	<sup>c</sup> Cont.
<i>M. caroli</i>	Control	Mean	1350.57	520.14	3.57	199.14	26.57	202.71	1870.71	0.77	2.86	1360.43	82.57	8.00
		S.E.	219.79	243.17	2.83	72.48	11.94	71.41	71.43	0.41	1.53	333.65	29.98	1.73
	LC odor	Mean	1645.67	258.67	7.00	152.67	36.00	159.67	1904.33	1.33	4.33	1425.50	47.00	7.50
		S.E.	187.39	192.09	2.24	119.74	14.37	120.45	114.52	0.94	2.62	422.94	18.84	0.85
	Total	Mean	1486.77	399.46	5.15	177.69	30.92	182.85	1886.23	1.03	3.54	1390.46	66.15	7.77
		S.E.	146.84	156.31	1.83	64.93	8.94	64.82	62.60	0.47	1.41	253.89	18.34	0.98
<i>A. agrarius</i>	Control	Mean	175.50	1804.38	21.75	31.50	66.88	53.25	1979.88	4.50	3.25	66.13	0.00	2.00
		S.E.	58.39	89.90	8.18	15.38	37.61	13.73	36.72	0.34	0.77	15.11	0.00	0.68
	LC odor	Mean	182.25	1436.63	61.00	365.50	54.63	426.50	1618.88	4.04	3.38	152.38	0.00	2.88
		S.E.	43.70	178.71	47.39	176.56	45.71	164.47	167.84	0.44	0.42	38.73	0.00	0.30
	Total	Mean	178.88	1620.50	41.38	198.50	60.75	239.88	1799.38	4.27	3.31	109.25	0.00	2.44
		S.E.	35.24	107.67	23.77	95.86	28.64	93.15	95.18	0.28	0.43	22.96	0.00	0.38
<i>R. exulans</i>	Control	Mean	789.36	846.27	53.00	390.82	20.55	443.82	1635.64	1.46	5.00	824.91	21.91	5.00
		S.E.	194.32	246.31	27.67	146.33	7.47	152.59	151.53	0.39	1.73	305.52	10.50	1.10
	LC odor	Mean	630.36	1078.00	8.00	376.82	6.82	384.82	1708.36	2.20	5.09	505.73	33.55	4.18
		S.E.	198.43	240.31	3.52	154.78	3.02	155.27	154.64	0.52	1.42	244.46	25.18	1.18
	Total	Mean	709.86	962.14	30.50	383.82	13.68	414.32	1672.00	1.83	5.05	665.32	27.73	4.59
		S.E.	136.63	169.81	14.47	103.94	4.21	106.42	105.94	0.33	1.09	194.08	13.37	0.79
<i>R. losea</i>	Control	Mean	897.13	389.00	447.75	261.13	105.00	708.88	1286.13	1.25	4.50	940.75	49.63	3.75
		S.E.	165.37	160.79	229.64	197.24	20.35	249.58	247.65	0.50	1.89	357.62	10.52	0.84
	LC odor	Mean	752.00	531.11	282.89	456.44	77.56	739.33	1283.11	1.03	4.67	629.44	2.56	4.11
		S.E.	190.22	178.76	117.25	301.47	29.07	269.04	256.03	0.34	1.41	279.09	1.53	1.07
	Total	Mean	820.29	464.24	360.47	364.53	90.47	725.00	1284.53	1.14	4.59	775.94	24.71	3.94
		S.E.	124.64	118.73	122.15	180.73	17.91	178.88	173.14	0.29	1.12	220.13	7.61	0.67
<b>Total</b>	Control	Mean	785.82	896.97	128.35	236.29	52.56	364.65	1682.79	1.99	4.03	783.88	35.76	4.62
		S.E.	108.53	135.93	60.60	69.25	11.72	85.75	86.97	0.32	0.78	160.16	8.72	0.65
	LC odor	Mean	736.29	873.03	93.06	355.68	41.94	448.74	1609.32	2.17	4.44	617.65	19.82	4.44
		S.E.	118.07	126.20	37.45	102.11	13.73	99.57	98.61	0.33	0.73	144.47	9.10	0.55
	Total	Mean	761.06	885.00	110.71	295.99	47.25	406.69	1646.06	2.08	4.24	700.76	27.79	4.53
		S.E.	79.64	92.06	35.42	61.66	8.98	65.41	65.40	0.23	0.53	107.52	6.33	0.42

**Notes:** LC odor = leopard cat odor group; Expl. = exploring, For. = foraging, Mot. = motionless, Conc. = concealing, Groom. = grooming, Def. = defensive, Non-def. = non-defensive, Cons.R. = consumption ratio, For. Ev. = foraging events, Lat. For. = latency to forage, Jump. = jumping, Cont. = contact. <sup>a</sup> Duration-based response (out of 2100 sec.); <sup>b</sup> amount (%); <sup>c</sup> number of occurrences. S.E. = standard error of mean.

**Table S2.4.** Behavioral responses of first trial only for the factor species, sex, and their interaction; and behavioral responses for the effects and interactions trial, treatment, and species. Significant values are displayed in bold.

Response	First Trial <sup>1</sup>			Both Trials <sup>2</sup>				
	Factor	Wald $\chi^2$	df	P	Factor	Wald $\chi^2$	df	P
<i>Consumption ratio<sup>a</sup></i>	Species	21.20	3	<b>&lt;0.001</b>	Trial	27.32	1	<b>&lt;0.001</b>
	Sex	4.19	1	<b>&lt;0.05</b>	Treatment	0.05	1	0.818
	Species × Sex	5.88	3	0.118	Species	90.46	3	<b>&lt;0.001</b>
					Trial × Treatment	0.35	1	0.553
					Trial × Species	8.38	3	<b>&lt;0.05</b>
					Treatment × Species	6.92	3	0.075
<i>Foraging events<sup>b</sup></i>	Species	21.24	3	<b>&lt;0.001</b>	Trial	1.32	1	0.251
	Sex	4.96	1	<b>&lt;0.05</b>	Treatment	0.70	1	0.403
	Species × Sex	12.68	3	<b>&lt;0.01</b>	Species	4.66	3	0.199
					Trial × Treatment	0.33	1	0.563
					Trial × Species	26.65	3	<b>&lt;0.001</b>
					Treatment × Species	0.37	3	0.947
<i>Latency to forage<sup>a</sup></i>	Species	29.41	3	<b>&lt;0.001</b>	Trial	26.17	1	<b>&lt;0.001</b>
	Sex	10.69	1	<b>&lt;0.005</b>	Treatment	0.02	1	0.878
	Species × Sex	4.73	3	0.193	Species	90.44	3	<b>&lt;0.001</b>
					Trial × Treatment	0.28	1	0.600
					Trial × Species	14.89	3	<b>&lt;0.005</b>
					Treatment × Species		3	
<i>Jumping<sup>b</sup></i>	Species	60.59	3	<b>&lt;0.001</b>	Trial	6.21	1	0.102
	Sex	3.86	1	0.052	Treatment	0.07	1	0.789
	Species × Sex	3.32	3	0.345	Treatment	0.05	1	0.825
					Species	67.30	3	<b>&lt;0.001</b>
					Trial × Treatment	0.30	1	0.584
					Trial × Species	0.33	3	0.847
				Treatment × Species	13.19	3	<b>&lt;0.005</b>	

**Notes:** <sup>1 a</sup> performed with GLM with gamma log-link function; <sup>1 b</sup> performed with GLM with negative binomial log-link function; <sup>2 a</sup> performed with GEE with gamma log-link function; <sup>2 b</sup> performed with GEE with negative binomial log-link function.

**Table S2.5.** Within-individual consistency in behaviors and significance of a random effect (ID) in linear mixed models of behavioral variables for individuals from all species (n = 68). Significant differences between models are based on log-likelihood ratio tests and displayed in bold.

Behavior	ID	Model	K	-2LL	Test	LRT	df	P	R
<i>Defensive</i>		1	1	2077.57					
	x	2	2	2067.14	1 vs. 2	10.43	1	<b>&lt;0.005</b>	0.378
<i>Non-defensive</i>		1	1	2091.13					
	x	2	2	2077.96	1 vs. 2	13.17	1	<b>&lt;0.001</b>	0.421
<i>Exploring</i>		1	1	2112.97					
	x	2	2	2095.87	1 vs. 2	17.10	1	<b>&lt;0.001</b>	0.473
<i>Foraging</i>		1	1	2154.56					
	x	2	2	2116.74	1 vs. 2	37.82	1	<b>&lt;0.001</b>	0.654
<i>Motionless</i>		1	1	1921.72					
	x	2	2	1896.59	1 vs. 2	25.13	1	<b>&lt;0.001</b>	0.557
<i>Concealing</i>		1	1	2064.02					
	x	2	2	2057.08	1 vs. 2	6.22	1	<b>&lt;0.05</b>	0.312
<i>Grooming</i>		1	1	1679.45					
	x	2	2	1675.97	1 vs. 2	3.48	1	0.062	0.224
<i>Consumption ratio</i>		1	1	528.83					
	x	2	2	505.12	1 vs. 2	23.71	1	<b>&lt;0.001</b>	0.544
<i>Foraging events</i>		1	1	788.00					
	x	2	2	777.99	1 vs. 2	10.01	1	<b>&lt;0.005</b>	0.371
<i>Latency to forage</i>		1	1	2222.45					
	x	2	2	2171.70	1 vs. 2	50.75	1	<b>&lt;0.001</b>	0.726
<i>Jumping</i>		1	1	1430.65					
	x	2	2	1393.55	1 vs. 2	37.10	1	<b>&lt;0.001</b>	0.649

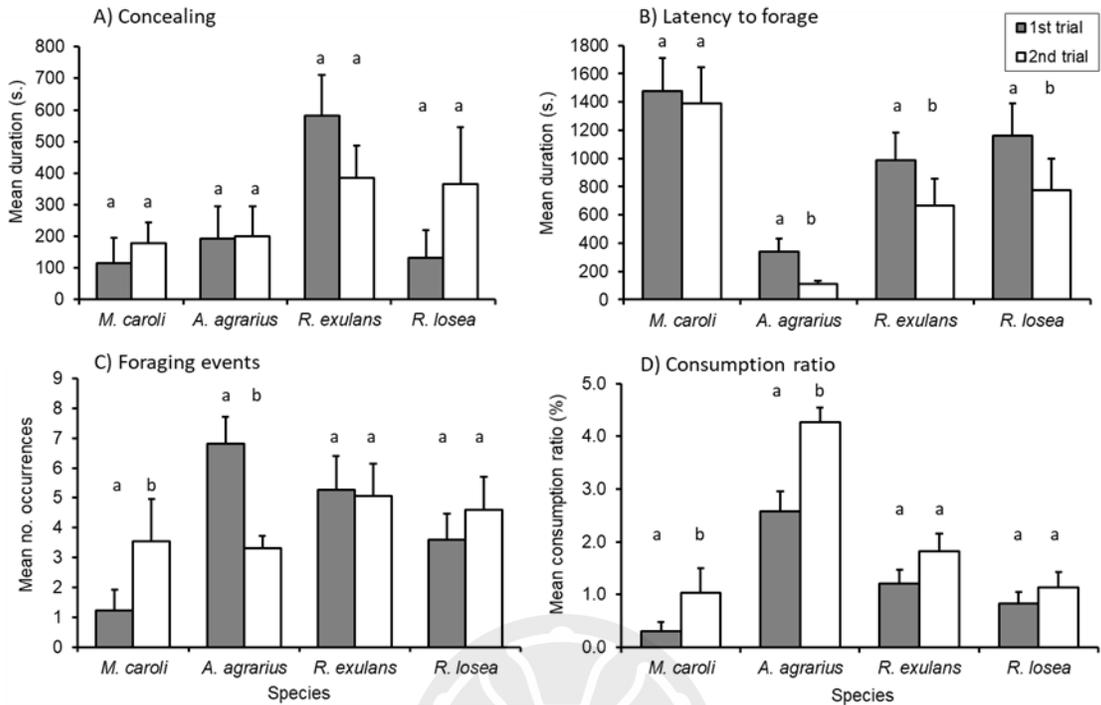
Notes: 'x' indicates a random effect included in a model. ID = individual identity, K = number of parameters, -2LL = -2 log-likelihood, LRT = log-likelihood ratio test. R refers to repeatability, estimated as  $R = V_i / (V_i + V_r)$ , where  $V_i$  is variance of the random effect (ID) and  $V_r$  is residual variance of the model.

**Table S2.6.** Within-individual consistency in behaviors and significance of a random effect (ID) in linear mixed models of behavioral variables for individuals from all species (n = 68). Species, treatment and trial included as fixed effects in both models. Significant differences between models are based on log-likelihood ratio tests and displayed in bold.

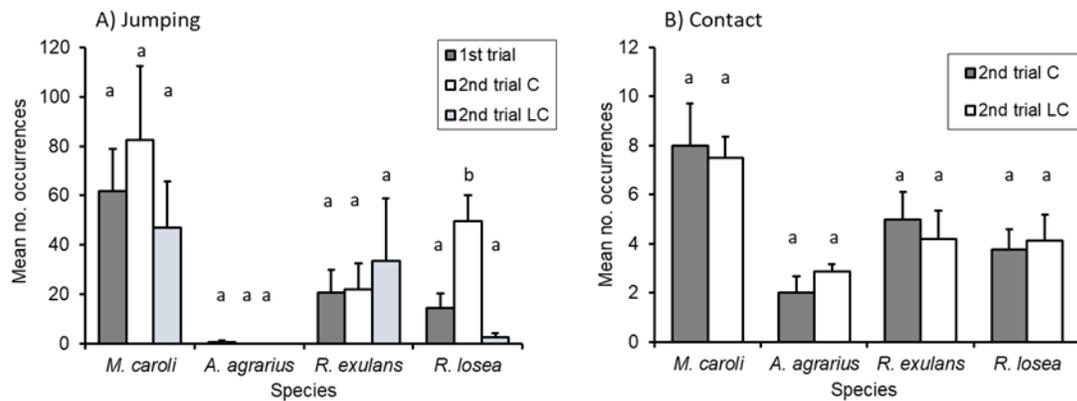
Behavior	ID	Model	K	-2LL	Test	LRT	df	P	R
<i>Defensive</i>		1	3	2001.18					
	x	2	4	1994.93	1 vs. 2	6.25	1	<b>&lt;0.05</b>	0.302
<i>Non-defensive</i>		1	3	2006.37					
	x	2	4	1998.84	1 vs. 2	7.53	1	<b>&lt;0.01</b>	0.330
<i>Exploring</i>		1	3	1981.93					
	x	2	4	1980.85	1 vs. 2	1.08	1	0.299	0.128
<i>Foraging</i>		1	3	2038.12					
	x	2	4	2011.60	1 vs. 2	25.62	1	<b>&lt;0.001</b>	0.576
<i>Motionless</i>		1	3	1820.40					
	x	2	4	1808.16	1 vs. 2	12.24	1	<b>&lt;0.001</b>	0.413
<i>Concealing</i>		1	3	1996.55					
	x	2	4	1991.77	1 vs. 2	4.78	1	<b>&lt;0.05</b>	0.266
<i>Grooming</i>		1	3	1599.23					
	x	2	4	1598.53	1 vs. 2	0.7	1	0.403	0.104
<i>Consumption ratio</i>		1	3	457.45					
	x	2	4	444.58	1 vs. 2	12.87	1	<b>&lt;0.001</b>	0.422
<i>Foraging events</i>		1	3	771.79					
	x	2	4	763.18	1 vs. 2	8.61	1	<b>&lt;0.005</b>	0.351
<i>Latency to forage</i>		1	3	2127.39					
	x	2	4	2129.42	1 vs. 2	47.35	1	<b>&lt;0.001</b>	0.716
<i>Jumping</i>		1	3	1367.16					
	x	2	4	1340.60	1 vs. 2	26.56	1	<b>&lt;0.001</b>	0.576

Notes: 'x' indicates a random effect included in a model. ID = individual identity, K = number of parameters, -2LL = -2 log-likelihood, LRT = log-likelihood ratio test. R refers to repeatability, estimated as  $R = V_i / (V_i + V_r)$ , where  $V_i$  is variance of the random effect (ID) and  $V_r$  is residual variance of the model.

## Figures



**Figure S2.1.** Mean duration (out of 2100 seconds) of behaviors A) Concealing and B) Latency to forage, number of occurrences of C) Foraging events, and D) Consumption ratio. Each response variable is compared between species and trial. Error bars represent standard error of the mean. Differences in letters above each species indicates significant differences based on post hoc analysis between 1st trial and 2nd trial for that species.



**Figure S2.2.** Mean number of occurrences of A) Jumping, and B) Contact. Jumping is compared between species, treatment group and trial. Contact is compared between species and treatment group. 1st trial comprises both treatment groups. ‘2nd trial C’ refers to the control group during the second trial. ‘2nd trial LC’ refers to the leopard cat odor group during the second trial. Error bars represent standard error of the mean. Differences in letters above each species indicates significant differences based on post hoc analysis between subgroups: 1st trial, 2nd trial C, 2nd trial LC.



## **Appendix B: Supplementary material for Chapter 3**

### **Figures**



**Figure S3.1.** Enclosed foraging containers in different microhabitat for seed consumption component of Experiment 1 (February 2020) in Miaoli County, Taiwan. The picture on the left shows an example of a covered station, and the picture on the right shows an exposed station. In both pictures the containers do not contain the contents of seeds and sand, which were used in the experiment.



## Appendix C: Supplementary material for Chapter 4

### Tables

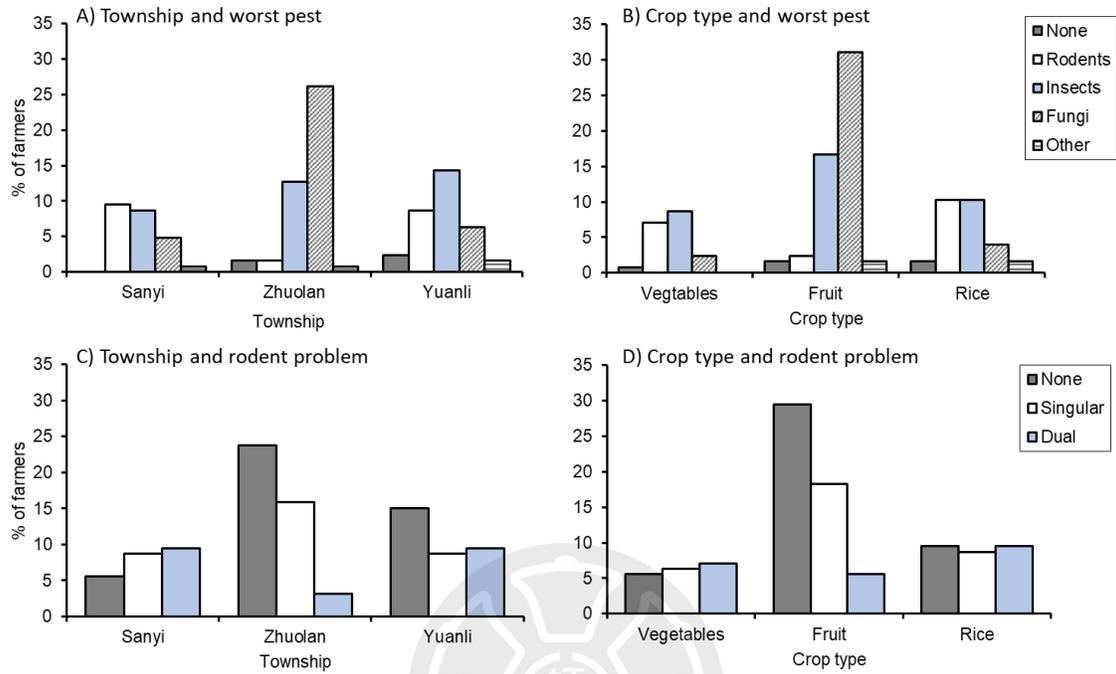
**Table S4.1.** Distribution of farmer pest control behaviors; use of rodenticides and pesticides, as well as mean Likert scores for statements (1-5), and agreement for perceived effectiveness, willingness to use less or stop using.

Behavior	n	Freq. (%)	Likert score	% of farmers		
				Disagree	Neutral	Agree
Use rodenticides	126	42 (33.3)				
Think they are effective	37		3.57	2.7	43.2	54.1
Willingness to use less	37		3.24	24.3	29.7	45.9
Willingness to stop using	37		2.70	51.4	24.3	24.3
Use pesticides	125	97 (77.6)				
Think they are effective	91		3.77	1.1	27.5	71.4
Willingness to use less	93		3.58	14.0	20.4	65.6
Willingness to stop using	93		2.62	52.7	28.0	19.4

**Table S4.2.** Spearman rank correlation matrix of farmers' willingness to change their rodenticide and pesticide usage. Significant values displayed in bold.

	Use less rodenticides	Stop using rodenticides	Use less pesticides	Stop using pesticides
Use less rodenticides	1			
Stop using rodenticide	0.669	1		
Use less pesticides	<b>&lt;0.001</b>		1	
Stop using pesticides	0.278	0.298	0.312	1
	0.111	0.087	<b>&lt;0.005</b>	
	0.310	0.582		
	0.075	<b>&lt;0.001</b>		

## Figures



**Figure S4.1.** Farmers' perceptions (%) of worst pest compared with A) township and B) crop type, and extent of rodent problem compared with C) township and D) crop type from the survey conducted in Miaoli County.

## Surveys

### English version of survey

#### Section 1: Background information about you and your farm

<b>Age:</b> <input type="checkbox"/> 18-25 <input type="checkbox"/> 26-35 <input type="checkbox"/> 36-45 <input type="checkbox"/> 46-55 <input type="checkbox"/> 56-65 <input type="checkbox"/> >65	<b>Gender:</b> <input type="checkbox"/> Male <input type="checkbox"/> Female
<b>Education</b> (Highest level completed): <input type="checkbox"/> Elementary school <input type="checkbox"/> Junior high school <input type="checkbox"/> High school <input type="checkbox"/> University (undergraduate degree) <input type="checkbox"/> Master's degree or higher	
<b>What is your main occupation:</b> <input type="checkbox"/> Farming <input type="checkbox"/> Other (please specify):	
<b>What is your primary source of income:</b> <input type="checkbox"/> Farming <input type="checkbox"/> Other (please specify):	
<b>Is your household dependent on your farming:</b> <input type="checkbox"/> Yes <input type="checkbox"/> No	
<b>How long have you been farming in this area (years):</b> <input type="checkbox"/> 1-10 <input type="checkbox"/> 11-20 <input type="checkbox"/> 21-30 <input type="checkbox"/> >30	
<b>Do you have livestock/ poultry:</b> <input type="checkbox"/> Livestock <input type="checkbox"/> Poultry <input type="checkbox"/> None	
<b>Do you have pet dogs or cats:</b> <input type="checkbox"/> Dog <input type="checkbox"/> Cat <input type="checkbox"/> None	
<b>If you do have pets, do they stay close to your crops/ agricultural fields:</b> <input type="checkbox"/> Yes <input type="checkbox"/> No <input type="checkbox"/> Uncertain	

<b>What crops do you grow:</b>
<b>What is the main crop you grow:</b>
<b>Do you have more than one farm:</b> <input type="checkbox"/> Yes <input type="checkbox"/> No. If yes, how many:
<b>Do you own or lease the land of your farm:</b> <input type="checkbox"/> Own <input type="checkbox"/> Lease
<b>Do you store your crops:</b> <input type="checkbox"/> Yes <input type="checkbox"/> No
<b>If you store your crops, do you store them in a cold temperature room:</b> <input type="checkbox"/> Yes <input type="checkbox"/> No

#### Section 2: Types of pests and extent of problem

1. **Instructions:** Please select which organism causes damage

	Rodents	Insects	Plants	Fungi	Other	None
This organism is a problem for my crops when they are growing	<input type="checkbox"/>					
This organism is a problem for my crops when I store them	<input type="checkbox"/>					
This organism causes the most damage overall to my crops ( <b>Please select only one</b> )	<input type="checkbox"/>					

2. What percentage of your annual yield of crops do you think are lost to pests? Approximately.

\_\_\_\_\_ %

### Section 3: Measures for pest control

**1. Instructions:** If you use rodenticides and/ or pesticides please indicate how you get them, your reasons for using them, and approximately how much you spend on them per year.

	Do you use them?	How do you get them? (Can select more than one)	What do you consider when choosing which to use? (Can select more than one)	How much money do you spend on them per year?
<b>Rodenticides</b>	<input type="checkbox"/> Yes <input type="checkbox"/> No (If no, please see question #2)	<input type="checkbox"/> Request from government officials <input type="checkbox"/> I buy them myself locally <input type="checkbox"/> I buy them myself online <input type="checkbox"/> Other: _____	<input type="checkbox"/> Availability <input type="checkbox"/> Price <input type="checkbox"/> Tradition <input type="checkbox"/> Effectiveness <input type="checkbox"/> What other farmers are doing <input type="checkbox"/> Environmental friendliness <input type="checkbox"/> Other people's health <input type="checkbox"/> Personal health <input type="checkbox"/> Other: _____	_____ NTD
<b>Pesticides</b>	<input type="checkbox"/> Yes <input type="checkbox"/> No (If no, please see question #3)	<input type="checkbox"/> Request from government officials <input type="checkbox"/> I buy them myself locally <input type="checkbox"/> I buy them myself online <input type="checkbox"/> Other: _____	<input type="checkbox"/> Availability <input type="checkbox"/> Price <input type="checkbox"/> Tradition <input type="checkbox"/> Effectiveness <input type="checkbox"/> What other farmers are doing <input type="checkbox"/> Environmental friendliness <input type="checkbox"/> Other people's health <input type="checkbox"/> Personal health <input type="checkbox"/> Other: _____	_____ NTD
If you use pesticides, do you use: <input type="checkbox"/> insecticides <input type="checkbox"/> herbicides <input type="checkbox"/> Fungicides <input type="checkbox"/> Other: _____				

**2. Instructions:** Please answer if you currently do NOT use rodenticides

Why do you currently not use rodenticides? \_\_\_\_\_

Have you used rodenticides before?  Yes  No

If yes, do you think they were effective?  Yes  No  Neutral

If yes, do you think rodents cause more damage to your crops now than when you were using rodenticides?

Yes  No  Uncertain

**3. Instructions:** Please answer if you currently do NOT use pesticides

Why do you currently not use pesticides? \_\_\_\_\_

Have you used pesticides before?  Yes  No

If yes, do you think they were effective?  Yes  No  Neutral

If yes, do you think pests cause more damage to your crops now than when you were using rodenticides?

Yes  No  Uncertain

4. Do you ever use traps for rodents?

Yes  No. If yes, what kind: \_\_\_\_\_

5. Have you ever used other methods other than rodenticides, pesticides or trapping to control pests?

Yes  No. If yes, please specify: \_\_\_\_\_

6. **Instructions:** Please indicate your level of agreement for each statement

	Strongly Agree	Agree	Neutral	Disagree	Strongly Disagree	Uncertain
Pests cause a lot of damage to my crops	<input type="checkbox"/>					
Rodents are a major pest for my house	<input type="checkbox"/>					
Rodents are a major pest for farming in my community	<input type="checkbox"/>					
I think rodents are a risk to people	<input type="checkbox"/>					

#### Section 4: Willingness to change pest control practices

1. **Instructions:** Please indicate your level of agreement for each statement

<b>Rodenticides</b>	Strongly Agree	Agree	Neutral	Disagree	Strongly Disagree	Uncertain
I think the rodenticides I use/ used in my community are effective	<input type="checkbox"/>					
I would be willing to use less rodenticides	<input type="checkbox"/>					
I would be willing to stop using rodenticides	<input type="checkbox"/>					
<input type="checkbox"/> I already do not use rodenticides						

2. **Instructions:** Please indicate your level of agreement for each statement

<b>Pesticides</b>	Strongly Agree	Agree	Neutral	Disagree	Strongly Disagree	Uncertain
I think the pesticides I use/ used in my community are effective	<input type="checkbox"/>					
I would be willing to use less pesticides	<input type="checkbox"/>					
I would be willing to stop using pesticides	<input type="checkbox"/>					
<input type="checkbox"/> I already do not use pesticides						

**3. Instructions:** If you are willing to use less/ stop using rodenticides and/ or pesticides, please indicate the reasons

<b>I would be willing to use less/ stop using for the following reasons:</b>	
<b>Rodenticides</b>	<input type="checkbox"/> Financial compensation <input type="checkbox"/> To protect the environment <input type="checkbox"/> To protect my health <input type="checkbox"/> To protect people's health <input type="checkbox"/> They are ineffective <input type="checkbox"/> Other: _____ <input type="checkbox"/> None. I am not willing to change the amount I use <input type="checkbox"/> I already do not use rodenticides
<b>Pesticides</b>	<input type="checkbox"/> Financial compensation <input type="checkbox"/> To protect the environment <input type="checkbox"/> To protect my health <input type="checkbox"/> To protect people's health <input type="checkbox"/> They are ineffective <input type="checkbox"/> Other: _____ <input type="checkbox"/> None. I am not willing to change the amount I use <input type="checkbox"/> I already do not use pesticides



## Chinese version of survey

### 第一部分：您和農地的背景資訊

年齡: <input type="checkbox"/> 18-25 <input type="checkbox"/> 26-35 <input type="checkbox"/> 36-45 <input type="checkbox"/> 46-55 <input type="checkbox"/> 56-65 <input type="checkbox"/> >65	性別: <input type="checkbox"/> 男 <input type="checkbox"/> 女
教育程度 (最高學歷): <input type="checkbox"/> 國小 <input type="checkbox"/> 國中 <input type="checkbox"/> 高中 <input type="checkbox"/> 大學 <input type="checkbox"/> 研究所以上	
請問您主要的職業是: <input type="checkbox"/> 農民 <input type="checkbox"/> 其他 (請說明):	
請問您主要的收入是: <input type="checkbox"/> 務農 <input type="checkbox"/> 其他 (請說明):	
請問你們家的生活是否依賴務農: <input type="checkbox"/> 是 <input type="checkbox"/> 否	
請問您在這個地區從事農作多久了(年): <input type="checkbox"/> 1-10 <input type="checkbox"/> 11-20 <input type="checkbox"/> 21-30 <input type="checkbox"/> >30	
請問您有養牲畜或家禽嗎: <input type="checkbox"/> 牲畜 <input type="checkbox"/> 家禽 <input type="checkbox"/> 都沒有	
請問您有養狗或貓嗎: <input type="checkbox"/> 狗 <input type="checkbox"/> 貓 <input type="checkbox"/> 都沒有	
如果有, 請問他們養在您的農地嗎: <input type="checkbox"/> 是 <input type="checkbox"/> 否 <input type="checkbox"/> 不確定	

請問您種植哪些農作物:
請問您主要種植的農作物是什麼:
請問您有很多塊農地嗎: <input type="checkbox"/> 是 <input type="checkbox"/> 否 若是, 請問有幾塊:
您耕作的土地是: <input type="checkbox"/> 自己的地 <input type="checkbox"/> 租來的
請問您會貯藏收成嗎: <input type="checkbox"/> 是 <input type="checkbox"/> 否
若您會貯藏收成, 請問是否放在低溫倉庫: <input type="checkbox"/> 是 <input type="checkbox"/> 否

### 第二部分: 有害生物和危害程度

#### 1. 請選會造成危害的生物:

	鼠類動物	昆蟲	植物	菌類	其他	沒有
這個生物在農作物生長期會造成問題	<input type="checkbox"/>					
這個生物在收成貯藏期會造成問題	<input type="checkbox"/>					
這個生物造成的問題最嚴重(請只選一項)	<input type="checkbox"/>					

#### 2. 請問有害生物造成的損失佔您一年收穫的百分之幾? 大約 \_\_\_\_\_%

第三部分: 危害防治作法

1. 請問：

	請問您有沒有使用?	請問您如何取得? (可以選不只一個)	請問您如何選擇要用哪種? (可以選不只一個)	請問您每年花多少錢在這上面?
毒鼠藥	<input type="checkbox"/> 有 <input type="checkbox"/> 沒有 (如果沒有, 前往第二題)	<input type="checkbox"/> 向公家單位索取 <input type="checkbox"/> 我在本地購買 <input type="checkbox"/> 我在網路購買 <input type="checkbox"/> 其他: _____	<input type="checkbox"/> 方便取得的 <input type="checkbox"/> 便宜的 <input type="checkbox"/> 一直在用的牌子 <input type="checkbox"/> 比較有效的 <input type="checkbox"/> 跟其他農民用一樣的 <input type="checkbox"/> 對環境友善的 <input type="checkbox"/> 不會影響人類健康的 <input type="checkbox"/> 不會影響我的健康的 <input type="checkbox"/> 其他: _____	_____ NTD
農藥	<input type="checkbox"/> 有 <input type="checkbox"/> 沒有 (如果沒有, 前往第三題)	<input type="checkbox"/> 向公家單位索取 <input type="checkbox"/> 我在本地購買 <input type="checkbox"/> 我在網路購買 <input type="checkbox"/> 其他: _____	<input type="checkbox"/> 方便取得的 <input type="checkbox"/> 便宜的 <input type="checkbox"/> 一直在用的牌子 <input type="checkbox"/> 比較有效的 <input type="checkbox"/> 跟其他農民用一樣的 <input type="checkbox"/> 對環境友善的 <input type="checkbox"/> 不會影響人類健康的 <input type="checkbox"/> 不會影響我的健康的 <input type="checkbox"/> 其他: _____	_____ NTD
如果您有使用農藥, 請問您使用的是: <input type="checkbox"/> 殺蟲劑 <input type="checkbox"/> 除草劑 <input type="checkbox"/> 殺菌劑 <input type="checkbox"/> 其他: _____				

2. 如果您目前沒有使用毒鼠藥, 麻煩幫忙回答以下的問題:

為什麼您目前沒有使用毒鼠藥? \_\_\_\_\_

您過去使用過毒鼠藥嗎?  有  沒有用過

如果有用過, 您覺得有用嗎?  有  沒有  普通

如果有用過, 您覺得目前的鼠類問題比以前嚴重嗎?  是  沒有  不清楚

3. 如果您目前沒有使用毒農藥, 麻煩幫忙回答以下的問題:

為什麼您目前沒有使用農藥? \_\_\_\_\_

您過去使用過農藥嗎?  有  沒有用過

如果有用過, 您覺得有用嗎?  有  沒有  普通

如果有用過, 您覺得目前的病蟲害問題比以前嚴重嗎?  是  沒有  不清楚

4. 請問您是否會用陷阱捉老鼠?

是  否。若是，請問您用的是何種陷阱：\_\_\_\_\_

5. 請問您曾經使用除了老鼠藥、殺蟲劑或陷阱以外的其他方式做危害防治嗎？

有  沒有。如果有，請具體說明：\_\_\_\_\_

6. 請問您是否同意：

	非常同意	同意	還好	不同意	非常不同意	不確定
有害生物造成我農作物非常大的損失	<input type="checkbox"/>					
我們家有老鼠的問題	<input type="checkbox"/>					
老鼠嚴重危害我們這裡的農業	<input type="checkbox"/>					
我認為老鼠對人造成風險	<input type="checkbox"/>					

#### 第四部份: 改變危害防治做法的意願

1. 請問您是否同意：

毒鼠藥	非常同意	同意	還好	不同意	非常不同意	不確定
我認為我們這邊用的毒鼠藥有用	<input type="checkbox"/>					
我會願意減少使用毒鼠藥	<input type="checkbox"/>					
我會願意停止使用毒鼠藥	<input type="checkbox"/>					
<input type="checkbox"/> 我已經沒有用毒鼠藥了。						

2. 請問您是否同意：

農藥	非常同意	同意	還好	不同意	非常不同意	不確定
我認為我們這邊用的農藥有用	<input type="checkbox"/>					
我會願意減少使用農藥	<input type="checkbox"/>					
我會願意停止使用農藥	<input type="checkbox"/>					
<input type="checkbox"/> 我已經沒有用農藥了。						

3. 請問：

因為下列原因我會願意減少或停止使用:	
<b>毒鼠藥</b>	<input type="checkbox"/> 有金錢補償 <input type="checkbox"/> 保護環境 <input type="checkbox"/> 保護我的健康 <input type="checkbox"/> 保護他人健康 <input type="checkbox"/> 效果不佳 <input type="checkbox"/> 其他： _____ <input type="checkbox"/> 以上皆非，我沒有打算改變毒鼠藥的使用。 <input type="checkbox"/> 我已經沒有用毒鼠藥了。
<b>農藥</b>	<input type="checkbox"/> 有金錢補償 <input type="checkbox"/> 保護環境 <input type="checkbox"/> 保護我的健康 <input type="checkbox"/> 保護他人健康 <input type="checkbox"/> 效果不佳 <input type="checkbox"/> 其他： _____ <input type="checkbox"/> 以上皆非，我沒有打算改變農藥的使用。 <input type="checkbox"/> 我已經沒有用農藥了。

